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ERRATA.

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Page 202, line 5 from bottom and in second footnote, *for* K *read* K_1.

Page 203, line 12 from top, *for* it *read* r.

Page 204, line 13 from top, *for* $\frac{R}{100} = \frac{W_2 - W_1}{W_1}$ *read* $\frac{R}{100} = \frac{W_2 - W_1}{\frac{W_1 + W_2}{2}}$

„ line 15 from top, *for* $\frac{\frac{L_1 + L_2}{2}}{W_1}$ *read* $\frac{L_1 + L_2}{W_1 + W_2}$

„ line 7 from bottom, *for* $\frac{L_2 - L_1}{L_1}$ *read* $\frac{L_2 - L_1}{\frac{L_1 + L_2}{2}}$

THE

NEW PHYTOLOGIST

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THE EVOLUTION OF PLANTS.

NO such interesting theoretical contribution to a subject which is of primary interest to all botanists, and indeed to all biologists, as that recently published by Mr. Church,[1] has appeared for many years. It is impossible to attempt in the limited space available a comprehensive review of the theses and arguments developed by the author, even if any one botanist had the necessary competence, for there is scarcely an important biological problem which Mr. Church does not raise. All we can do here is to call attention to some of the fascinating expositions and speculations of the author, and indicate certain points of possible criticism. At the same time we would strongly recommend all botanists to obtain and read this work for themselves. It is rather hard reading, for the author's style is none too easy. He has a fondness for long and rather involved sentences, but he never fails to arouse interest and to stimulate thought and imagination. The price, in these days, is almost ridiculously cheap; for the same matter, printed with wider spacing and on a smaller page would easily fill a fair-sized volume. The work contains in fact about 60,000 words, more or less—the length of an ordinary "six shilling" novel, now costing seven shillings, at just half the price—while to the biologist it is more entertaining, and much better worth reading than most novels. Though often involved, the style is lively throughout, and Mr. Church's castigations of those who have had the misfortune to express opinions with which he disagrees, or to take what he considers a narrow view, to see the subject "out of perspective," never fail to amuse. The author's polemic, though often expressed in the language of almost contemptuous scorn, has the happy quality of leaving no poisoned sting behind. And this, though the author

[1] A. H. Church. *Thalassiophyta and the Subaerial Transmigration.* (Oxford Botanical Memoirs, No. 3), pp. 95, 3s. 6d. net., Oxford University Press, 1919.

is not always fair to those he criticises, occasionally misrepresents them, and is not infrequently slightly irritating to the reader, by reason of his air of Olympian detachment.

The first thesis is that just as the higher land plants have inherited their fundamental cell mechanism from primeval phytoplankton, so they have inherited the external form and segmentation of their bodies and the most fundamental tissue differentiations, from phytobenthon, *i.e.* from fixed, branching and leaf-bearing seaweeds, with radial organization, "Fibonacci" sequence of members and apical meristem. The author regards as inconceivable the idea that land plants have produced an equipment so parallel to that of marine algæ, as leaf and stem, parenchymatous tissues and radial organisation, in response to conditions so different from an aquatic environment as those of subaerial life. As a working hypothesis of evolution "the antithetic theory," he says, "is better than nothing at all; and for fifty years[1] it has dominated the botanical outlook (1851-1908) and has afforded an effective stimulus to research. The only effective criticism is the establishment of an alternative point of view; and those to whom the surprising adventures of an intercalated 'post-sexual phase' may not appeal, are naturally expected to provide something more rational." There have been many to whom these "surprising adventures" have made no appeal, nor have there been wanting attempts to present "an alternative point of view"—one was published in this Journal in 1907—though no doubt they were poor things beside the magnificent sweep of Mr. Church's exposition.

The author then proceeds to explain how the antithetic theory of alternation was rooted in the course of development of botanical research in the middle of the nineteenth century. "To Hofmeister, working at Leipsig and Heidelberg, in ignorance of the Sea, the progression of plant life was viewed from the *standpoint of the freshwater pond*, and in the light of a transition from the medium of fresh water and seasonal vegetation to the arboreal vegetation of the North Temperate zone, as displayed in Central Europe." The contempt for marine algæ shown by so eminent a biologist as Schleiden in 1849 is well brought out by a

[1] Though in a certain sense broadly true this statement is open to criticism. Hofmeister's doctrine was not specifically antithetic. The antithetic doctrine began with Celakovsky (1868), and gained no widespread acceptance till Bower's paper of 1890 gave it a definitely evolutionary significance. Nor has the antithetic theory dominated the botanical outlook unchallenged. Cf. Scott (1896).

quotation from the "Grundzüge." But it should be noted that while this ignorance of the rich and marvellous vegetation of the sea by the "land botanist" may explain the absence of any serious attempt to go to seaweeds for light on the evolution of land plants, it has nothing to do with "antithetic "as opposed to "homologous" alternation. The author ignores Pringsheim (1856, etc.)

The second thesis is that there is no probability of plant life having migrated from the sea to the land, viâ estuaries and rivers to freshwater swamps, and that the origin of land plants from marine forms took place by what the author calls *transmigration*,[1] *i.e.* the slow emergence of land from the sea, carrying with it a plant population. The migration viâ inland waters the author thinks impossible because of the deficient food supply in the form of salts, and he points out that all freshwater algal vegetation is in fact diminutive in size (starved and stunted) as compared with that of the sea. The diminished food-supply of such habitats would lead to a serious diminution in output of reproductive cells and hence in failure to compensate the wastage of the race, and to ultimate extinction. Only inferior (unicellular and filamentous) forms could survive under such conditions, and we must look for the ancestors of the main land vegetation among massive forms comparable with the best equipped modern seaweeds.

In considering the possibility of the transformation of a massive seaweed into a land plant we have first to envisage the actual change of conditions involved, in their effect on the vegetative economy, the day-to-day life of the plant. First of course we have the localisation of water supply and of the supply of the essential elements of the "food salts." Of these the second is by far the most insistent, since the author calculates that over 150 litres of sea water would have to be passed through the plant in order to obtain sufficient nitrogen to make one gram of aqueous plasma (taking the nitrogen content of the sea—the original nutritive medium—as one part in ten million). This proportion of water to combined nitrogen, however, is progressively decreased as we pass to soils containing more humus. "A progressively sub-saturated atmosphere with attendant desiccation, now appears as a blessing in disguise," as enabling the plant to get rid of this enormous quantity of excess water, at the same time stimulating the flow of the current. Meanwhile increased insolation, and increased facility of gaseous exchange, immensely

[1] The fitness of this word to express the hypothetical phenomenon in question is not very clear.

overstimulates the formation of carbohydrate, which cannot be used in building new protoplasm because of the limited supply of the necessary food salts, and thus leads to the deposition of immense quantities of waste polysaccharide—a condition which reaches its extreme in tree trunks and in the thick walled tissue of xerophytes generally. The change to subaerial land life, in fact, while immensely facilitating gaseous exchange[1] and therefore the constructive processes depending upon it, severely restricts the formation of new protoplasm, which can only be carried on by absorption of a great excess of water, so that the body of a land plant is much more largely composed of dead substance than is that of a submerged seaweed.

"The algæ of the transmigration," says the author, "may be roughly visualised as having possessed the metabolic efficiency of the Chlorophyceæ, the somatic equipment [parenchymatous structure and body segmentation] of the Phæophyceæ, and a reproductive scheme of life history more advanced than that of *Dictyota*, though in other respects falling behind that of the modern Florideæ, in that these last have eliminated the flagellated zoïd as microgamete in favour of a simple method of spermatogamy. The algæ of the transmigration may be thus said to have combined the best features, as factors of the highest grade of progression, of the known great conventional series of marine phytobenthon, and yet to have belonged to none of them."

Mr. Church conceives of the condition for the evolution of such forms in the slow rise of the sea bottom to benthic conditions, *i.e.*, to within range of light penetrating from the surface. Thus emerges the conception of a *benthic* or *seaweed epoch* of the world's history, which followed upon the earlier *plankton epoch* in which the ocean covered the surface of the globe to a uniform depth.[2] In the benthic epoch marine vegetation culminated in the shallow water areas of incipient continents. The marine benthon existing to-day, rich as it is in variety and development, is regarded as being a mere impoverished remnant of the benthic age, since it is confined to restricted portions of the very narrow *littorals* of the continents, and, together with the great bulk of the forms of the benthic age, the actual ancestors of the land plants have completely disappeared.

[1] Mr. Church is under the impression that the transmigrant to subaerial life is under *worse* conditions for obtaining carbon dioxide than a water plant. He seems to have got his data on the rate of diffusion wrong.

[2] That the ocean ever did so cover the globe must be regarded as questionable.

Later on the conditions for the evolution *en masse* into land plants of the green highly developed benthon whose characters have been indicated were presented by the rise of the incipient continental areas above sea level. The land thus first exposed was not covered by more or less deep deposits of soil, the results of long continued subaerial denudation, but consisted of bare rock surfaces, bearing, according to the theory, great masses of marine vegetation. Copious precipitation and a saturated atmosphere may be reasonably postulated, but the supply of nutritive salts, supposed to be present in the primeval ocean, would be entirely cut off, unless we postulate a low tide-wave with periodic return, or wetting within the range of the "splash."[1] The emerging surface would however shortly be covered with the remains of dead forms which had *not* survived the first stage of the transmigration, and the organic débris so produced would form the first (an organic) soil, from which the soil as we know it would be evolved by the gradual accumulation of the products of subaerial denudation. This organic débris would remain saturated in a saturated air, and would furnish the substratum from which the transmigrants would have to obtain their food.

And now we come to the weakest part of the author's exposition—his account of the way in which the vegetative bodies of these transmigrants became actually adapted to land life. Admitting that his general considerations are sound, and that his analysis of the factors is correct, we find no convincing picture of the actual transformation. Mr. Church conceives that the various types of algal organisation originating in the sea maintained their essential characters after the transmigration. Plankton forms remained plankton, even if they became "cryoplankton" or "dendroplankton": filamentous forms remained filamentous; and the more massive parenchymatous forms retained their cellular organisation which formed a basis for further adaptation. Thus we have the picture of comparatively massive forms capable of standing up by themselves (comparable with the Fucaceous *Cystoseira*) having an initial advantage on this account and being able by their massive structure to resist desiccation; increasing their deposits of "polysaccharide" (cellulose) as a result of the greater insolation;

[1] Here it may pertinently be asked: What is the probability that the primeval ocean had anything like the salt content of the sea as we know it to-day? The *original* ocean must have consisted of water condensed and recondensed on the cooling surface of the globe, and thus destitute of salts. How and when did it acquire its existing salt content?

initiating a subaerial "balancing mechanism" (geotropism); starting a root system by the boring down into the organic débris of the substratum of the massive "crampon system" (such as we see to-day in *Fucus* and *Turbinaria*) with vestiges of the "trichome system" surviving as root hairs; and a stele by lignification of the central cells of the axis, the peripheral "phloem" and secondary meristematic activity being already indicated among the massive brown seaweeds. This is all very well, but it is extraordinarily difficult to visualise exactly how, and by what stages it happened and the author gives us little help in this respect.

In writing of reproductive structures in relation to the transmigration Mr. Church is particularly interesting. He regards the archegonium as "clearly an end-product of oogamic evolution, the limiting term of something quite unknown, probably originating in something quite different from any recent archegonium, and, if we saw it, scarcely recognizable as such," "very probably of polyphyletic origin." He points out that in so far as the archegonium is a means of obtaining fertilization *in situ* for an oosphere, whose post-sexual nutrition involves a parasitic diploid embryo, it shares these characters with the egg-bearing organs of Florideæ, and hence such phenomena are part of the reproductive equipment evolved in the sea. The origin of the archegonium, as we actually know it, must therefore be sought in the transmigrant phyla, as a result of adaptation to the new conditions. But if, the author argues, fertilisation *in situ* had been developed *during* transmigration, the archegonial "oospore" would have been utilised as a resting phase, as happens in the transmigrants *Chara*, *Vaucheria*, etc., whereas in fact it always develops directly.

The origin of the archegonium and of the antheridium he seeks in a multicellular branchlet of the algal body, represented in the Phæophyceæ by the "multilocular" gametangium, thus following the line indicated by B. M. Davis (1903), though Church insists on the importance of the distinction between the algal gametangium liberating autotrophic zoïds and the antheridium of Archegoniates, whose zoïds have to be fed as well as protected from desiccation during development. Added to this we have the further transmigrant mechanism of dehiscence by turgescent terminal wall-cells on supply of free water. Church calls attention to the "primitive" features of the archegonium of *Sphagnum*, the most alga-like moss, and develops the analogy of the archegonium with the female organ of *Chara*, a transmigrant which tried to solve, with

indifferent success, the same problem that the Proto-archegoniate solved satisfactorily. The "exaggerated" neck of the archegonium the author compares with the pseudostylar micropyle of certain Gymnosperms and the stylar tube of Angiosperms.

Thus the essential features of the archegonium and of the antheridium appear an evolution of a multicellular fertile algal branchlet (the first beginnings of which appear in *Dictyota*), in response to the conditions of subaerial life, obtaining incidentally the advantages of the oogamy and of fertilisation and development *in situ*, advantages which the Florideæ (and *Chara*) in part have obtained in other ways.

The archegonium is polyphyletic in origin, and never existed in a condition of completely submerged algal benthon. Not only the Bryophytes but also different phyla of Pteridophytes are to be traced back to distinct origins, not only among marine benthon, but to distinct flagellate plankton ancestors. This conclusion was already suggested by the work of Bohlin and Luther (1897-1901) on the zoospores of algæ, though few students of the Archegoniatæ have been bold enough to follow out its full consequences, which involve the derivation from distinct flagellate types, not only of Ferns and Lycopods but also of Equisetales, and perhaps of *Isoëtes*, though the octokont zoïd of this genus may be derived from the isokont type. The whole trend of modern morphological investigation, indeed, encourages us not to be afraid of postulating far-reaching extension of independence of origin with convergence and homoplasy; and such postulates may justifiably be carried to a point which would have scandalised the older morphologists.

The origin of the archegonium and antheridium is only one problem raised by a consideration of the evolution of the reproductive mechanism of the green land plants. The sporogonium of the Bryophyte Mr. Church regards as the reduced form of a benthic radially organised shoot, from which, he thinks, the leaves have disappeared, leaving the photosynthetic mechanism on the axis. He strongly upholds Bower's contention that radial organisation is primitive, and insists that it originated as a response to the benthic conditions of life, since it is the common type among seaweeds. Dorsiventrality in land plants, for instance in the dichotomous dorsiventral liverworts, he regards as an evidence of degeneration or perhaps of derivation from degenerate dorsiventral seaweeds. The photosynthetic and transpiratory structures of sporogonia must either have been evolved independently of the corre-

sponding structures in the leaves of the sporophytes, or be regarded as relegated to the axis when the leaves of an originally leaf-bearing sporogonium disappeared. The latter hypothesis, to which Mr. Church inclines, seems gratuitous. Why should the leaves have disappeared completely leaving no trace? Is not the hypothesis of independent origin of the photosynthetic mechanism both simpler and fully justified on the general principle of homoplasy?

The "immersed" archesporium of the sporogonium (and equally of the sporangia of Pteridophyta) is to be taken as a layer of potential tetrasporangia, a tetrad being the characteristic limiting term of the benthic unilocular sporangium in which the meiotic mechanism determines the number four. Such immersion is commonly met with in the stichidia of the bulkier Florideæ, and the later complications of the central portion of the axis (columella) and of the peripheral "wall" found in the larger sporogonia of the mosses, are merely further modifications, while degeneration is illustrated in the smaller forms culminating in the simple sporogonium of *Riccia*. In the Pteridophytes "the view of a continuous stratum of archesporial cells being normal for older fern-laminæ, followed by the progression of sorus-restriction, and the localization of smaller patches to a system of more elevated out-growths (sporangia), as secondary emendations for wind-dispersal," forms part of Bower's account of the evolution of the sporangium. But the aerial wastage of spores is far greater than the marine wastage—Mr. Church estimates it in *Aspidium* at about 1000 times that of the Laminarian—and to meet this the spore-producing surface increases vastly in bulk, culminating in the tree ferns (*Alsophila*, up to 60 feet high).

This enormous wastage is quite overcome in the heterosporous forms, where spore production is brought into immediate relation with the production of gametes already economised by the archegonial mechanism; and the prothallus, which through its precocious juvenile sexuality is already far more efficient than the large sexual plant as a means of obtaining quick returns in the reproduction of the race, is still further economised, and the necessary duration of its life shortened, by inclusion in the spore. The culmination of this process in the seed plants, where there is no wastage at all of sexual cells as such, and a minimum of wastage of microspores (pollen grains) and thus of male gametes when the insect pollination mechanism is brought to the greate pitch of perfection, is familiar ground.

On the broadest biological grounds, Mr. Church thinks the plant kingdom should be classified as follows:—

Thalassiophyta	{	Plankton.
		Benthon.
Xerophyta	-	Xerophyton.

Xerophyta include not merely land plants but all plants which have a "water problem" in their economy and all freshwater forms which have survived the subaerial transmigration, to grow as best they can in media other than that of the sea.

Such, in very brief and incomplete outline, are some of the main features of Mr. Church's story of the evolution of the leading series of plant life on the earth. The outstanding feature of the story is the insistence on the large marine algæ as presenting us with various combinations of the factors, a selection of the best of which were employed in the adaptation to land life, and the corollary that only by a much more detailed and intensive study of seaweeds, can we obtain more positive knowledge of these factors. The characteristic merit of the author's contribution to the subject, is his insistence on the widest possible outlook, on a broad consideration, in the light of all the known facts, physical, chemical and physiological, as well as structural, of the necessary conditions of evolution of land plants from water plants. There can be little question that our view-points in comparative morphology have been too narrow and academic, and it is all to the good to be taken into a freer atmosphere. The writer may be forgiven if he finds in the stimulating atmosphere of Mr. Church's memoir one more evidence of the urgent necessity of escape from the bonds of our one-sided academic morphology in current teaching, and of laying far greater stress on a study of the physical and chemical conditions of life in its various forms. It is beside the point to reproach Mr. Church because he presents no new body of facts. He wants us to consider the facts we have in a saner manner, and to let the results of such consideration direct fresh research. Nor can we expect, as Mr. Church points out, to obtain fresh evidence on these points by searching for new fossils, exceedingly interesting as discoveries of new and simpler types of Pteridophytes, such as the recently described *Rhynia*, may be. It is overwhelmingly improbable that the original transmigrants which were the actual ancestors of our land flora have been preserved in fossiliferous rocks. We can only infer their characters, and that in the most general way, from a study of the structure and conditions of life of existing forms.

Once land plants were thoroughly established they must have acquired the general characters with which we are familiar, and the evidence of this or that variant on the type—one among thousands that must have existed—can tell us nothing significant about the general problem.

There are some points in Mr. Church's story that are doubtful or obscure. For instance he postulates a uniform ocean two miles deep on the surface of the earth as the medium in which the plankton phase of life was evolved and developed its perfection. The benthon age was made possible only by the approach of the sea bottom to the surface of the water as a preliminary to the emergence of continents. Geophysicists are not however agreed that this was the course of events. Some hold that there may have been land surfaces before the world was cool enough to support life. The "orthodox" biological view is that life arose in the warm water along the littoral and not as plankton in a uniform ocean. Unless we have a sound physical basis for the belief in the existence of a uniform ocean before land appeared the hypothesis of a plankton age preceding the benthon age is not necessary. Life may have originated as plankton, but we cannot be certain a priori that it did. There is also the question of the history of the content in mineral salts of the water of the primeval ocean.

We shall be glad to publish criticisms or remarks on the subject of Mr. Church's memoir, which raises, as was said at the outset, so many questions of the first biological interest.

A. G. T.

PHYLOGENETIC CONSIDERATIONS ON THE INTERNODAL VASCULAR STRANDS OF *EQUISETUM*.

By Isabel M. P. Browne.

[With Seven Figures in the Text].

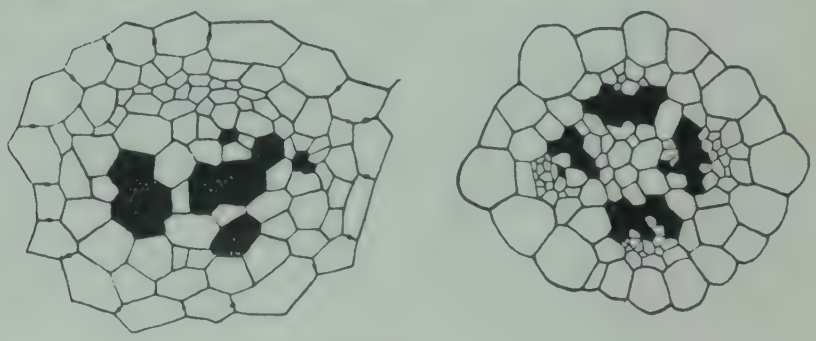
THE descriptions in the text-books of the vascular strands in the internodes of *Equisetum* are somewhat meagre and inadequate. In discussing the structure and nature of these strands it will be convenient provisionally to use the word bundle for them individually, without thereby prejudging their morphological nature.

Campbell (5, p, 464) figures such an internodal bundle of the aerial shoot, probably of *E. maximum*, Lam., for in the figure are to be seen the conspicuous tannin cells characteristic of this species. His drawing shows very clearly not only the carinal canal, with the remains of the carinal group of protoxylem adhering to its margin, but also the two lateral groups of metaxylem, situated near the periphery of the bundle and separated from the carinal canal by five or six cells. Curiously enough, his description makes no mention of these lateral groups of metaxylem. A rather fuller account of the internodal vascular bundles, including a description of the well-known carinal group of protoxylem and the two separate lateral groups of metaxylem, was given by Professor Bower (p. 386[1]) in his *Origin of a Land Flora* in 1908. Professor Bower in his description and discussion uses the word axis and of his three figures of internodal bundles, copied from Pfitzer in Rabenhorst's *Kryptogamen-Flora*, two are from the rhizomes of *Equisetum litorale*, L., and *E. silvaticum*, L., and the third from the aerial stem of *E. palustre*, L. His description, though brief, is thus a general one. It may perhaps be pointed out that the words internodes of the axis cover a wider field than that to which Professor Bower's description applies. The bundles of the subterranean tubers and those of the primary axis are also, in part of their course, internodal axial bundles and Professor Bower's description is inapplicable to them.

Subterranean tubers have been recorded from several species, and figures of their vascular bundles have been published for *E. arvense* by Milde (12, Pl. 1, Fig. 22) and by Ramey (15, Pl. 6,

[1] The small white space in the metaxylem-group on the reader's left is an intercellular space, not a parenchymatous cell.

Fig. 3), for *E. maximum* and *E. silvaticum* by Leclerc du Sablon (11, Figs. 15 and 17), and for the fossil *Equisetum* (or *Equisetites*) *stellare* Fritel and Viguier, from the Sparnacien by Fritel and Viguier (8, Text-Fig. 5 and Pl. IX, Fig. 3). Text-Fig. 1 *a* represents such a bundle of the tuber of *E. silvaticum*. It is copied from Leclerc du Sablon and the xylem is shown in black, in order to bring out its distribution more clearly. Except those of *E. arvense*, all the bundles of tubers that have been figured show essentially the same irregular distribution of tracheides, interspersed with small groups or bands of parenchymatous cells, though in the bundle of the fossil *Equisetites stellare* the cells, vascular and parenchymatous, are more numerous. According to Milde's figure the bundle of the tuber of *E. arvense* is also of this type, but in Ramey's figure of such a bundle the xylem consists of a solid group of 16 thick-walled tracheides.



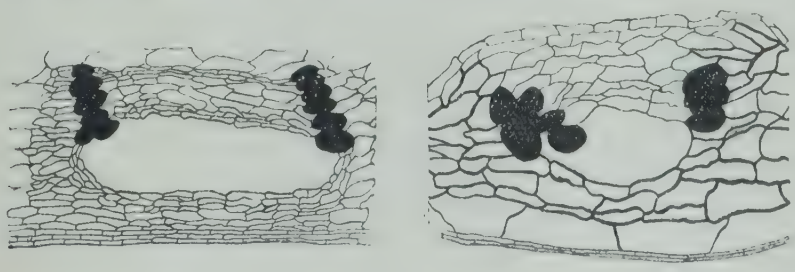
a. *b*.

Text-Fig. 1. (*a*) Transverse section of a vascular bundle of a tuber of *E. silvaticum*, after Leclerc du Sablon. Magnification not stated. (*b*) Transverse section of the third internode of the primary axis of *E. maximum*, er Buchtien. ×216.

In the internode of the primary axis the xylem of each bundle forms a single group. This is shown in Text-Fig. 1 *b*., representing a transverse section of an internode of the primary axis of *E. maximum*, Lam. The figure is copied from Buchtien (4, Pl. 5, Fig. 119) and again the xylem has been filled in in black. The wood of each of the small bundles consists of five to ten, on average of eight tracheides. In the more reduced bifascicular primary axis of *E. variegatum*, figured by the same author, each bundle contains four or five rather small tracheides, irregularly embedded in parenchyma (4, Pl. 5, Fig. 118).

But even in the internodes of the aerial stems of *Equisetum* the structure of the bundle is not always uniform. For the two postero-lateral groups of metaxylem are not always separated from the more deeply-seated carinal group of protoxylem. A study of

Milde's figures of the internodal bundles of the aerial stems shows tha in *E. mexicanum*, Milde, *E. Schaffneri*, Milde and *E. lævigatum*, A. Braun the lateral bands of metaxylem abut on the carinal canal and are, therefore, in connection with any of the earlier-formed tracheides which may persist at the edge of the carinal canal. Text-Fig. 2 *a.* and *b.*, adapted from Milde (12, Pl. 23, Fig. 7 and Pl. 32. Fig. 5) show this condition in the two last mentioned species. Milde's figures of similarly situated bundles in *E. Martii*, Milde and *E. giganteum*, L., though unsatisfactory, because drawn on a very small scale, seem to show that in these species also the lateral bands of metaxylem are, sometimes at least, in contact with the canal resulting from the disorganization of the first-formed tracheides (12, Pl. XX, Fig. 3, and Pl. XXI, Fig. 4). Again, Milde's figures of the internodal bundles of the aerial axes of *E. xylochætum*, Mett. and *E. debile*, Roxb. show that in these species one of the lateral groups of metaxylem may come into contact with the edge of the carinal canal, while the other may

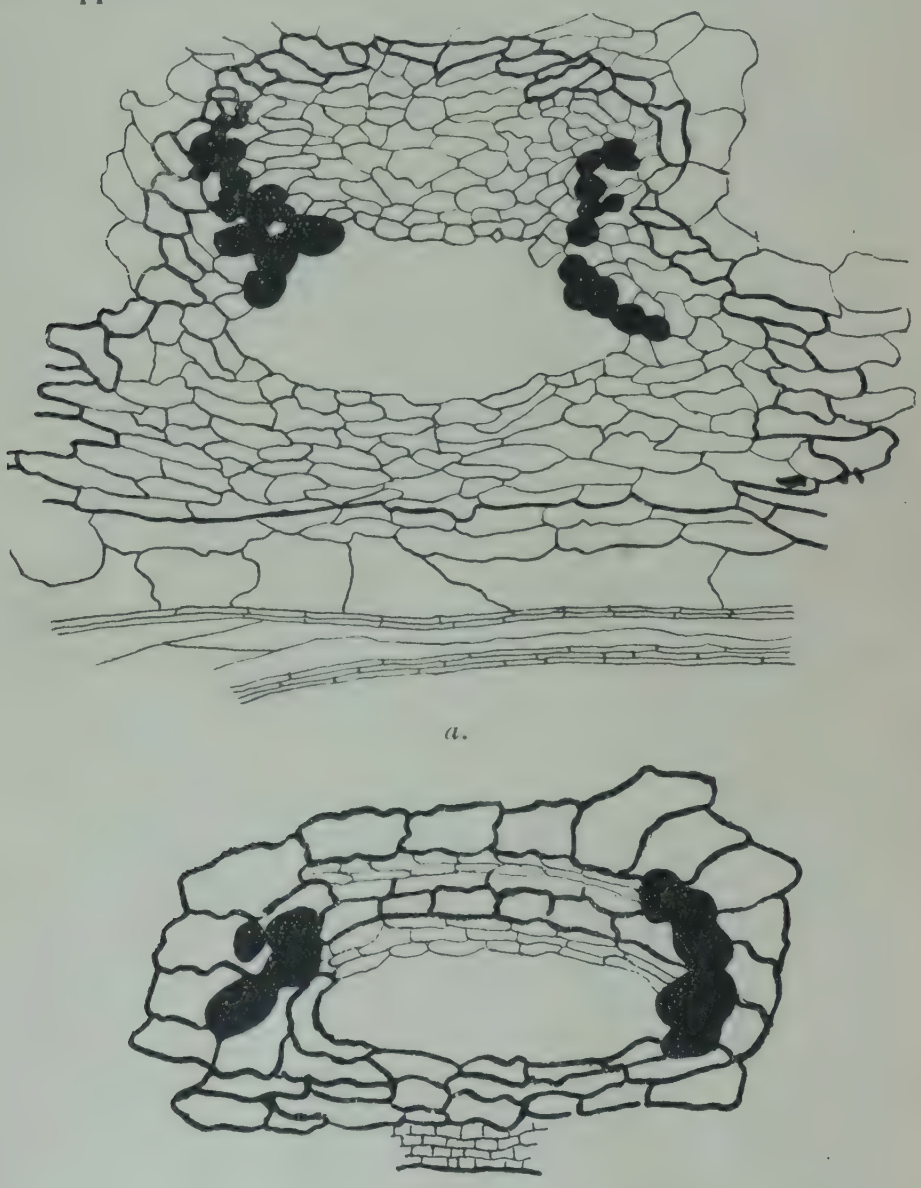


a. *b.*

Text-Fig. 2. (*a*) Transverse section of the vascular bundle of the aeria stem of E. *Schaffneri*, after Milde, × 176. (*b*) Transverse section of the vascular bundle of the aerial stem of *E. laevigatum*, after Milde, × 176.

remain separated from it either by a single parenchymatous cell or by a few such cells. Text-Figs. 3 *a.* and *b.* are adapted from Milde's figures of such bundles in *E. xylochætum* and *E. debile* respectively (12, Pl. XIX, Fig. 8 and Pl. XXVI, Fig. 17). Quéva (14, p. 23) has remarked that in *E. litorale* Kühlew the vascular bundles below the node assume a remarkable appearance owing to the linking up of the lateral bands of metaxylem at the edge of the carinal canal. His figure 21 shows that this species possesses locally a bundle which is essentially similar to the types of bundle depicted in Text-Fig. 2 and 3. Text-Fig. 4 *a.* is from a preparation of one of the upper internodes of the cone-bearing stem of *Equisetum giganteum*. The lateral groups of metaxylem are here almost in contact with the carinal canal; between them lies an irregular band of tracheides, broken in the middle and on one side

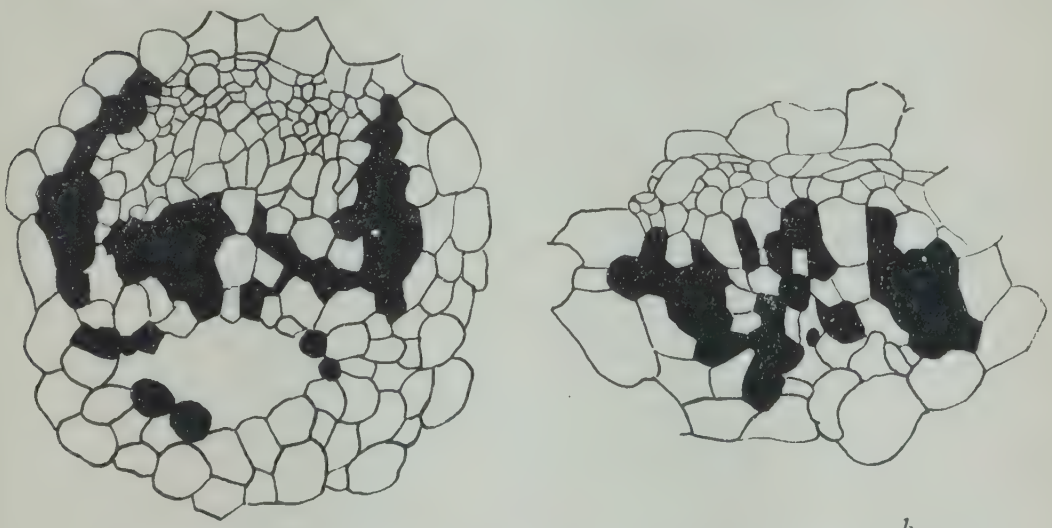
by parenchymatous cells; the band is roughly parallel to the carinal canal. This figure illustrates the fact that there is some variety in the way in which the lateral metaxylem groups approach or become linked up with the carinal group; in some cases they first approach one another.



TEXT-FIG. 3. (*a*) Transverse section of the vascular bundle of the aerial stem of *E. xylochætum*, after Milde, × circa 100. (*b*) Transverse section of the vascular bundle of the aerial stem of E. debile, after Milde, × circa 460.

The structure of the cone is now known in detail in four species, *viz.*, *E. arvense*, L., *E. palustre*, L., *E. limosum*, L., *E. maximum*, Lam. In none of the cones of these species do the

vascular bundles of the internodes[1] show a separation of the xylem into three distinct groups. In the internodes of the cones of all these species (Browne 2 and 3) the vascular tissues may be disposed in single separate bundles—*i.e.*, in strands which at the node above give off the vascular supply of one sporangiosphore—or in bands giving off at the next node, traces to two or more sporangiosphores. As the vascular strands in the internodes of the vegetative axes are always single bundles it will be convenient in the subsequent discussion to select single internodal bundles of the cone rather than bands for comparison with other internodal, axial bundles. The structure of the bands is similar in essentials to that of the single bundles, but the former are, naturally, considerably wider than the latter.



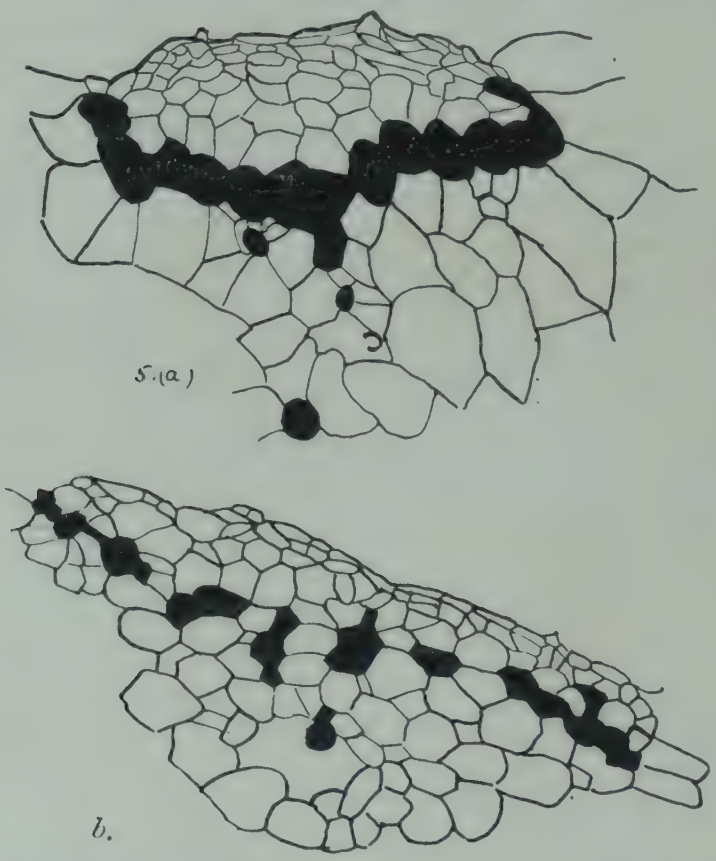
a. *b.*

Text-Fig. 4. (*a*) Transverse section of small vascular bundle of upper part of fertile stem of *E. giganteum*, × circa 250. (*b*) Transverse section of small vascular bundle in one of the internodes of the cone of *E. giganteum*, × circa 325.

Text-Fig. 5 *a* represents such a bundle, rather a small one, just below the lowest whorl of sporangiophores in *E. arvense*. Except that higher up the slight outward concavity of the xylem is replaced by a slight inverse curvature, so that the band of xylem conforms to the curve of the periphery of the stele, and that there is, in the example figured, a single large, possibly centripetal tracheid in the pith internal to the carinal canal, this bundle is

[1] The words internode and internodal bundles are here used, for convenience sake, to denote the axis of the cone between the sporangiophores and the bundles at levels where the latter are not giving off traces. The use of the term is not intended to imply a true homology between a vegetative node and the axis of the cone at the insertion of the sporangiophores, since this depends upon the undecided and highly controversial question of the morphological nature of the latter.

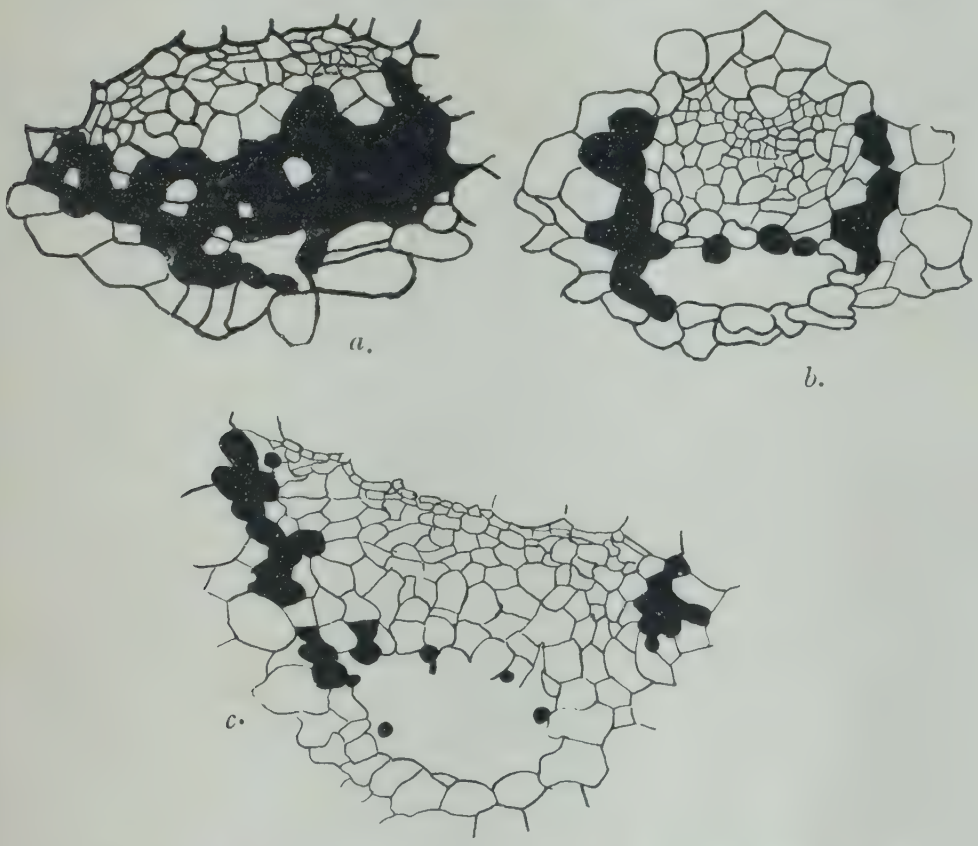
quite typical of the internodal bundles of the cone. These bundles show considerable variations. Often the more or less transverse band of xylem is in contact with a small central group of tracheides slightly further in. Though there is usually no definite carinal canal the internal tracheides are often torn, especially towards the base of the cone. Often there are also other little groups of small tracheides internal to the main transverse band of wood and



TEXT-FIG. 5. (*a*) Transverse section of small vascular bundle of *E. arvense*, just below lowest whorl of cone, × circa 245. (*b*) Transverse section of small vascular bundle of *E. maximum*, just above the insertion of the annulus, × circa 250.

adherent to it or separated from it by a cell or two. The transverse band of xylem is typically one cell in depth, but locally it may be two or more cells in radial extent. It is often broken by a parenchymatous cell or small group of such cells. A markedly greater development of this interruption of the main band of tracheides is characteristic of the cone of *E. maximum*. Text-Fig. 5 *b*, though actually drawn from a bundle just above the level of the annulus, is quite characteristic of many cone-bundles. In this species the carinal canals, though decreasing in size, are often

persistent through the lower internodes of the cone. The bundles in the internode of the cone of *E. palustre* are very much like those of the cone of *E. arvense;* but though varying somewhat they are on average markedly narrower and their xylem tends to attain a very slightly greater depth radially. In the internodal bundles of the cones of *E. limosum* and *E. hiemale* the xylem is of no greater radial extent than in the similarly situated bundles of *E. arvense*, and the bundles themselves are, typically, quite as narrow as those of *E. palustre*. Those of *E. giganteum* have a considerably greater



TEXT-FIG. 6. (*a*) Transverse section of vascular bundles of *E. giganteum*, just below insertion of annulus, × circa 250. (*b*) Transverse section of vascular bundle of *E. giganteum* from axis just below the insertion of the annulus × circa 200. (*c*) Transverse section of small bundle of *E. arvense*, between the insertion of the annulus and the lowest whorl of sporangiophores, × 200.

radial depth of xylem, as may be seen in Text-Fig. 4 *b*, representing a small bundle of the internode of the cone of this species. In the fully developed bundle of this species the xylem is usually five to six, not uncommonly seven to eight cells in depth, so that the wood forms oval masses, sometimes broken up by or enclosing parenchymatous cells.

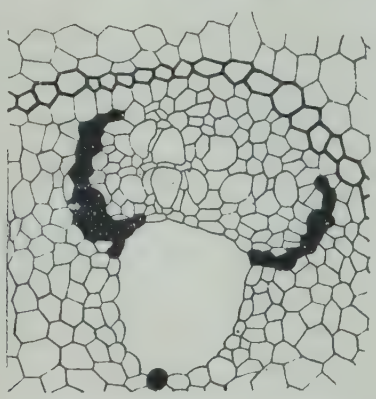
As a rule the transition from the bundle with two metaxylem groups to the type of bundle characteristic of the cone occurs a little above the annulus. In *E. giganteum*,[1] presumably correlated with the vascularization of the annulus, the change occurs a little below the insertion of the annulus; so that in this species the bundles just below the annulus much resemble the bundles of the internode of the cone (cf. Text-Fig. 6 *a*, of a bundle in this region with Text-Fig. 4 *b*). Usually the lateral bands of metaxylem become united with any persistent tracheides of the carinal group, and when this linking up is completed we get for a time a distribution of the xylem of the bundles recalling strikingly that found in the bundles represented in Text-Fig. 2 *a* and *b*. Text-Fig. 6 *c* shows a phase in this process in a bundle of *E. arvense*. Here one of the lateral groups of metaxylem has spread almost as far as the edge of the carinal canal, while the other has hardly increased in size or changed in outline. Text-Fig. 6 *b*, is of a bundle of *E. giganteum*, a little way below the insertion of the annulus, before the xylem has assumed the form characteristic of the internodal bundles of the cone.

We may now consider very briefly the structure of the bundles in the internode of the rhizome. So far as I have been able to ascertain, there is only one case recorded from the rhizomes of existing Equiseta in which the lateral groups of metaxylem show any approach to the carinal group of tracheides. Such an approach occurs, according to Quéva, in the rhizomes of *E. litorale* (14, p. 30), where the lateral metaxylem is only separated by a single cell from the protoxylem adhering to the carinal canal. It is by no means surprising that examples of bundles in which the lateral metaxylem is sufficiently well-developed to approach close to or to come into contact with the protoxylem are rare in the rhizome; for Quéva has shown that the metaxylem is generally less well developed in this region. Indeed, according to him, it may sometimes be completely wanting from the rhizomes of *E. maximum* and *E. limosum* (14, p. 30). Milde's figure of a part of the rhizome of *E. pratense* shows three bundles, one without any lateral metaxylem and two with a single metaxylem-tracheide on one side and none on the other (12, pl. VII, Fig. 9). Milde also figures a bundle without lateral metaxylem from the rhizome of *E. maximum* (12, Pl. IV, Fig. 1), though his figures of other bundles of the rhizome of this species show the lateral metaxylem

[1] The structure of this cone is more fully described in a paper soon to be published in the *Annals of Botany*.

quite well. The same author figures too a bundle of the rhizome of *E. silvaticum* in which the lateral metaxylem is represented by a single element on each side (12, Pl. IX, Fig. 9). According to Quéva there is often only a single element of metaxylem on each side of the bundles of the rhizomes in *E. maximum* and *E. limosum* (14, pp. 29-30).

In the only fossil rhizome of *Equisetites* the internal structure of which has been elucidated, that of *E. noviodunense*,[1] the elements composing the lateral bands of metaxylem are exceptionally numerous (in the bundle figured 11-17 in each band) and each group of metaxylem extends from near the periphery of the bundle to the edge of the carinal canal (8, Text-Fig. 7 and Pl. 9, Fig. 2). Text-Fig. 7 is copied from a schematic figure of such a bundle



TEXT-FIG. 7. Transverse section of the vascular bundle of the rhizome of *Equisetites noviodunense*, after Fritel and Viguier. Magnification not given.

given by Fritel and Viguier. As in the other Text-Figs. of the present paper the xylem is filled in in black.

Reduction of the lateral groups of metaxylem is not confined to the rhizome. Milde figures a bundle of the aerial stem of *E. trachyodon* in which one of the lateral groups of metaxylem is developed in a typical manner and the other is totally absent (12, Pl. XXXIII, Fig. 15). I have noticed that commonly in *E. limosum* lateral metaxylem is not present in the bundles for a part of the region lying between the last whorl of leaves and the annulus. Just below the level of insertion of the annulus, and on the breaking up of the nodal ring of wood, lateral metaxylem is present; but in the four cones of which I have made serial sections of this region it is absent from the bundles for a varying distance betwe en these two points. In the anatomically very different cone of *E. giganteum* I have also observed in some cases the absence and

[1] The tubers described as *E. stellare* were probably born on the rhizome of this species.

in others the very poor development of the lateral metaxylem at this level. In this species, however, the lateral metaxylem groups may be well-developed over the whole of the region between the last whorl of leaves and the point, just below the insertion of the annulus, at which the xylem of the bundles assumes the more compact form characteristic of the axis of the cone.

We may now ask which among the types of internodal bundle found in *Equisetum* is the most primitive. These bundles belong to five principal types. The first, that with a solid mass of xylem, is found, so far as we know, only in some of the tubers of *E. arvense*; the second, in which xylem and parenchyma are irregularly intermingled in an oval or circular mass, is characteristic of some of the tubers of *E. arvense* and of all the tubers of other species the internal structure of which is known to us. Thirdly, there is the well known type of bundle consisting of a central protoxylem group and two postero-lateral groups of metaxylem. Then there is the form of bundle in which these two lateral groups are absent or very poorly developed. Lastly there is the type of internodal bundle in which the xylem is more or less continuous, though its outline varies. Often, especially in the aerial axis, the xylem-strand is U-shaped, with protoxylem at the innermost point. In other cases, *e.g.*, usually in the cone, the xylem represents the segment of a circle, often very narrow radially, and with one or more groups of small elements at or near its inner edge.

It seems clear that the tubers are modified rhizomatous branches, adapted for purposes of storage, and it can hardly be doubted that their bundles are cœnogenetic in character. They are interesting in that they show that the bundle consisting of three separate groups of xylem is not universal throughout the internode, even of the better known European species of the genus. It seems natural to regard the tubers as modified storage branches of the rhizome and their bundles as phylogenetic derivatives from the bundles of the rhizome. Duval-Jouve, indeed, has induced the production of branches below the whorl of leaves that forms a crown to the tubers. He found that if the tubers were grown in very wet earth they produce branches that grow into rhizomes; but that if grown in water and exposed to the light, the branches developed as aerial axes (6, p. 6—7). It is probably significant that though Fritel and Viguier give a list of eleven extinct, tuber-bearing fossil species of *Equisetum* (or *Equisetites*), the oldest being the Triassic *E. Mougeoti* Brgnt. and *E. arenaceum* (Jaeger) Bonn, yet no definite tubers have

been recorded from the characteristic palæozoic Equisetales, the Calamariæ. It is true that a few years ago Mr. Kidston (10) figured and gave a short description of what he termed a "rhizomatic tuber," belonging to an undetermined Calamite of Westphalian age. In this case, however, the tuber consists in three swollen internodes of a rhizome, the other internodes of which appear to be unaffected. This certainly seems a less specialized condition than the development of "chaplets" of tubers or of special branches as single tubers. It should noted that Duval-Jouve figures a rhizome of *E. arvense* in which a single internode is swollen and tuberous (6, Pl. I, Fig. 2).

Again, the type of bundle in which the lateral metaxylem is absent, or reduced to a cell, seems clearly to have arisen by reduction of the metaxylem from the bundle with three separate groups of xylem. Between this last-mentioned type of bundle and that with continuous xylem there exists, as has been shown above, a fairly complete series of intermediate forms. We can hardly doubt that one of these types has arisen from the other. Which, then, is the more primitive? The question is one of some importance, for, if the three groups of xylem have arisen in the phylogeny by the breaking up of a single mass of xylem, owing to the failure of certain cells to develop as tracheides, then the whole bundle is, as has been recently claimed by Eames (7, pp. 593-524), clearly a phylogenetic unit.

It seems to me that the arguments in favour of the priority of the bundle with continuous xylem are very strong. In the first place such priority would assume the gradual reduction of the bundle in the Equisetaceæ, and few, if any botanists, would now dispute the proposition that the existing species of *Equisetum* are reduced forms. There can be little question but that some of the Mesozoic *Equisetites* were among the ancestors of the recent genus *Equisetum*; and these mesozoic fossils show, on the whole, a diminution in size as we pass up from the older to the more recent rocks. Secondly, it is clear that in the rhizome the vascular tissues are, on the whole, markedly more reduced and it is here that we find hardly any indications of the continuity of metaxylem and protoxylem. I certainly regard it as significant that in the only fossil rhizome of which we possess a detailed anatomical account the lateral metaxylem is more highly developed than in the recent forms and is continuous with the protoxylem. This rhizome, known as *Equisetites noviodunense*, comes from the Sparnacien, and it would seem that at this geological horizon the reduction of the vascular tissues, even in the rhizome, had not

brought about the separation of the xylem of the bundle into three groups. Unfortunately the aerial axes of this species are unknown; but it seems probable that in them too the xylem of the bundle was continuous. A third argument in favour of the priority of the bundle with more or less continuous xylem over that in which the wood forms three separate groups, lies in the fact that the latter type of bundle is never found in the cone. Now, it is a well known and widely accepted generalisation, that reproductive are more conservative than vegetative axes. Further, bundles with continuous xylem are characteristic of the primary internodal axis of *E. maximum*, the only one with which we are acquainted except that of *E. variegatum*, the bifascicular stele of which is clearly reduced. Again, though from the phylogenetic point of view a knowledge of the internal structure of the Mesozoic Equisetales is much to be desired, we possess numerous descriptions of the axes of the palæozoic Equisetales, the Calamariæ, and, in no case, so far as I am aware, is there any evidence for the existence of bundles with three groups of xylem.

It is suggested, then, that the type of bundle which is usually regarded as the typical internodal form has arisen in the phylogeny from a bundle in which the xylem was continuous, owing to the failure of some of the cells of the metaxylem to develop as tracheides. It would seem that in most cases, at least, the mass of xylem had become U-shaped before its fragmentation. It is quite probable, however, to judge from the varied position of the lateral metaxylem groups (these may be divergent, parallel or even convergent) and from the differences in their outline, that the persistent tracheides have, in some cases, undergone a certain shifting in position since their separation from the protoxylem. Usually, apparently, the cells which ceased to develop as tracheides seem to have been those near the carinal group, *i.e.*, those at the bend of the U. But Quéva has pointed out that when in the rhizome of *E. maximum* or *E. limosum* a lateral metaxylem-group is reduced to a single tracheide, this is often in contact with the carinal canal (14, p. 30). Here, then, the cells which fail to develop as tracheides are the outer elements of the metaxylem. I have noticed that in *E. giganteum*, in the part of the axis between the annulus and last whorl of leaves, in which, as already noted, lateral metaxylem may be wanting or much reduced, a single large tracheide not infrequently represents the only metaxylem present, and that it may abut on the carinal canal, or be situated at the periphery of the bundle. In fact, while reduction of the xylem of the bundle seems generally to

have been caused by the obsolescence of the elements of the metaxylem abutting on the protoxylem-group, any of the elements of the metaxylem may cease to develop as tracheides. This is only what we should expect in view of the fact that sometimes there is no lateral metaxylem.

If we accept the view that the lateral groups of metaxylem are parts separated from the protoxylem relatively recently in the phylogeny, the question as to whether these lateral groups contribute to the formation of the trace seems of less importance. It is possible to reconcile the late Mr. Gwynne-Vaughan's denial of the existence of this contribution (9) with Mr. Eames' assertion of such a contribution (7, p. 593) by supposing that the metaxylem may contribute to the trace if the latter is unusually large or the carinal group of protoxylem relatively less well-developed, while in other cases the carinal group of tracheides may itself suffice for the emission of traces.

We have not so far discussed the vexed question of the direction of lignification of the lateral groups of metaxylem. The fact that, more often than is usually believed to be the case, they are not separate from the carinal canal is not, of course, incompatible with their centripetal development. Still, very possibly, but for their supposed independence from the protoxylem, the late Mr. Gwynne-Vaughan might never have asserted their probable homology with centripetal xylem. This author did not mention, possibly he overlooked, an earlier assertion than his of the centripetal development of the lateral strands of wood. Poirault, in a paper read as early as 1887, and published in 1890, stated that the lateral xylem of the bundle of *Equisetum* developed centripetally (14, p. 13). It is true that he called this lateral wood "secondaire"—a misleading expression, for to judge from his description he does not regard the lateral tracheides as being formed by a cambium, but merely uses the word "secondaire" to bring out the contrast between the metaxylem and the protoxylem, the elements of which he describes as "primary vessels." Since the first publication of Mr. Gwynne-Vaughan's views, however, have appeared Quéva's excellent figures of developmental stages of the metaxylem. The latter's very careful descriptions, based on material giving remarkably complete series of stages, seem to show that the lateral metaxylem develops centrifugally (15), though probably, as pointed out by Mr. Eames (8, p. 592), there is some irregularity in development.

The nature of the ring of short reticulate tracheides known as the nodal, or more accurately the supra-nodal xylem, is one which

can only be very briefly touched upon here. After Quéva's researches there seems every reason to regard it as primary (15, p. 21). In that case it may represent a fresh development of wood, or, as seems to me more likely, it may be a modification of the ordinary primary centrifugal xylem of the axis. But whether it be regarded as a modification or a fresh development, it is difficult not to connect its retention during reduction of vascular tissues, or its development, with the presence of numerous appendages at the node. In such British species as I have examined, and in the small cone-bearing branches of *E. giganteum*, I have never seen any indication of the separate existence of the lateral strands inside and over the ring of reticulate nodal tracheides, which Mr. Gwynne-Vaughan claims to have observed in the nodes of *E. giganteum*. But such persistence of the lateral bands would not be incompatible with the phylogenetic unity of the Equisetaceous bundle. The fact that such a large number of appendages requiring vascular supply are initiated, even though they are not always fully developed, at most of the nodes of the vegetative axis of *Equisetum*, in spite of the relatively poor development of xylem in the internodes of these axes, has hardly received the attention that it deserves.[1] As regards the usual position of the lateral metaxylem of the internode it may be pointed out that the vascular supply of the branches is inserted on the ring of xylem vertically above the point at which two adjacent groups of metaxylem, each belonging to a different bundle, have fused. It seems not unlikely that the position of the persistent metaxylem at the sides of the bundle is correlated with the need for emission of a vascular supply to the branches, each of which lies midway between two leaf-traces. In this connection it is significant that the tendency of the lateral metaxylem to reduction—a tendency sometimes leading to complete abortion—is relatively pronounced in the rhizome, where comparatively few branches develop. Again, in *E. limosum* and sometimes in *E. giganteum*, the internode below the annulus seems to contain little or no metaxylem. It is possible that this observation should be brought into relation with the fact that at the reduced node of which the annulus marks the position (Browne, 2 and 3), no lateral branches are normally developed or even initiated. In other words, if, as seems to be established, the annulus is a reduced leaf-sheath, the reduced node at which it is inserted probably lost the capacity to

[1] The frequent presence, in unbranched or poorly branched axes, of numerous dormant branches, provided with a fully developed vascular supply, seems to show that reduction, or loss, of branching is a recent character in the phylogeny of the genus.

initiate branches relatively early in the phylogeny; and correlated with this loss certain species have ceased, or are ceasing, to produce lateral metaxylem in this region.

Perhaps, even to-day, it is not useless to add that in expressing the conviction that the internodal strands of *Equisetum* are phylogenetic units that may conveniently be termed bundles, it is by no means intended to suggest that these strands are in any strict, scientific sense equivalent to the ordinary internodal bundles of the Angiosperms. The fact that such bundles are common, whereas, in *Equisetum*, the bundles contain some purely cauline vascular elements, constitutes a real difference between the two types. Moreover, it seems particularly gratuitous to seek for strict stelar homologies between groups so remote from one another and of such very different antiquity as the Equisetales and the Angiosperms.

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MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER I.

Introduction.

THE adoption of experimental methods of evolutionary study early in the present century was accompanied by sanguine hopes that a general and universally applicable method of evolution might thus be discovered. But two decades of intensive experimental work with plants and animals has led to a greater diversity of opinion concerning evolutionary factors than ever before. Wherever a particular species or group of forms has been intensively studied, the results have illuminated a particular field of inquiry concerning evolution. But other results, dealing with organisms having different bionomic relations, have answered other questions and at the same time propounded new series of problems. While there has therefore been a great accumulation of data concerning the variations of organisms, the inheritance of characters new and old, and the relations and reactions of these organisms to their varied environments; yet this has led to no unitary result which can be universally applied. These experiments have rather served to emphasize the manifold character of the evolutionary process.

Not only have various groups of organisms contributed their quota to this multifarious result, but different methods of experiment and different fields of observation have no less clearly tended to emphasize particular evolutionary factors. Individual bias has also of course played a part in the interpretation of many results.

Important and valuable as these experimental studies have been in opening a new era of evolutionary investigation, and leading to very definite conceptions concerning heredity and many aspects of variation and distribution, yet I believe they have been perhaps most generally useful in a direction which has not as yet been recognized. For their very variety, apart from interpretations put upon them, is sufficient to show that in the search for one all-explanatory evolutionary principle, man is following an *ignis fatuus*. Darwin recognized this even in his day, for while he laid chief stress upon natural selection, he also relied upon the Lamarckian factor,

and to some extent on the direct effect of environment. But Darwin's followers at the end of the nineteenth century, having eliminated other factors, were endeavouring to show that natural selection was sufficient to account for all the then known phenomena of variation and adaptation. In the meantime palæontologists and anatomists, particularly the American School of Neo-Lamarckians, had kept alive the Lamarckian factor. Following that period, the striking discoveries in connection with mutations and Mendelian inheritance opened up a new outlook.

Darwin made no clear distinction between continuity and discontinuity in variation or inheritance, although his language sometimes clearly implies that he had observed one thing or the other. In some cases infinitesimal variations were apparently in his mind in writing, but when he refers to "individual differences" it is usually clear that he is citing what we should now call small or parvigrade (Poulton) mutations. In one aspect then, mutation as an evolutionary factor represents a refinement and an increased precision in the application of Darwin's theory of natural selection. That he recognized the occurrence of variations which were not necessarily subject to natural selection is clear from such passages as the following in the "Origin": "I am inclined to suspect that we see, at least in some of these polymorphic genera (such as *Rubus*, *Rosa*, *Hieracium* and fossil Brachiopods), variations which are of no service or disservice to the species, and which consequently have not been seized on and rendered definite by natural selection" (p. 33).

If we go but a step further, and assume that these variations are followed by others in the same population with elimination of some steps by selection; or if we assume the immediate origin of new specific types through single mutations, and their gradual spread from the centre of origin, then we are using the mutation theory of de Vries as it is widely applied at the present time. Darwin's objections to "sudden and considerable deviations of structure" as material for evolution, were based largely upon his observations of wide saltations and monstrosities. They included the well-known argument of swamping through crossing, which has since been negatived by the Mendelian discoveries.

It cannot then be said that the present Mendelian-mutationist attitude in its general aspects represents more than a refinement of Darwin's main thesis, based upon greatly increased knowledge of variation, inheritance, and cell structure; and a restriction of

the incidence of natural selection. Nevertheless this increased precision is of vast importance, because it is based upon a multitude of actual breeding experiments and accurate observations.

But while mutationist conceptions have been coming in as a refinement of Darwinism, other elements of the problem have not been left without attention. Much has been written concerning isolation, the adaptation of geographic races, and orthogenesis; while even crossing has been raised by some to the importance of an evolutionary factor. While these pages are primarily a discussion of mutation as an evolutionary factor, an incidental consideration of some of the other factors will be necessary, in order to give mutation its proper setting in the picture.

As mentioned above it appears probable that the era of the vain search for a single evolutionary principle is now at an end. That end has been chiefly brought about by the experimental researches in genetics on the one hand and the work of animal palæontologists on the other. While palæobotanists have been actively accumulating valuable historical data, it does not appear that palæobotany has yet much direct evidence to offer concerning the causes or methods of evolution in plants. The reason for this probably lies in the greater difficulties of method involved in palæobotanical research. The animal palæontologist may be able to determine or identify an animal from the mere outline of a single bone or a few portions of the skeleton. The fossil botanist must rely largely upon sections of material which is so preserved as to show the details of histological structure.

All the known evolutionary factors have in turn had their advocates, who usually attempted to make their application universal. We have had the Lamarckian factor of use and disuse, natural selection, isolation, direct adaptation ("epharmosis"), orthogenesis, mutation, the unpacking of Mendelian factors, and crossing, as explanatory principles. Their failure in universality has been apparent enough in every case. On the other hand, many of these factors and perhaps all, may be reasonably claimed to have had some share in the evolutionary result. Each advocate may be expected to press his claim as far as possible, but there are obvious limiting factors with regard to every one of these principles the moment we begin to examine them; and it is only by limiting the field of vision or deliberately closing our eyes to other facts, that a belief in the universal application of any one of them can be retained.

Any future evolutionary principle which aspires to universality must consist in a synthesis or integration of these factors, or such of them as can be proved to be sound in the fields of their application. The time for unlimited advocacy of single exclusive factors is past. Future advance in the understanding of evolution must then consist in the determination of the limitations of each factor, and the weaving together of such elements as are sound, into a connected whole.

The recent attempt of Osborn (1918) to deal with organic evolution from the energy standpoint, while not as yet markedly successful, may perhaps represent a line of approach through which a synthesis of evolutionary factors, may ultimately be reached. Whitman's (1919) elaborate studies of evolution in pigeons are grounded upon energy conceptions. The great accumulation of palæontological material which has taken place in recent years, gives vertebrate palæontologists a solid substratum of fact on which to construct hypotheses, which experimentalists can no longer afford to ignore. Gaps in mammalian phylogenies, for example, have been filled up to a remarkable extent, so that many of the older arguments drawn from the imperfection of the geological record are no longer applicable. The wonder is rather at the completeness, variety, and abundance of the skeletons preserved in deposits and unearthed by man.

A re-reading of the *Origin of Species*—an exercise which any biologist could profitably indulge in, at least once in every five years—serves on the one hand to emphasize the greatness of Darwin's vision, and on the other to encourage the present scientific man by showing the immense accumulation of accurate knowledge concerning organisms which has taken place since Darwin's time. The problem of to-day, just as it was in 1859, is to bring all these facts to bear upon the explanation of the diversity of organic species. In connection with this task not one of the modern biological sciences can be safely ignored, and such physical sciences as astronomy, geo-morphology, physiography, chemistry and many aspects of physics must be pressed into service. Darwin dealt with variation in wild and domesticated animals and plants; heredity; the relations of organisms to each other and to their inorganic environment, hybridization and sterility; the geological record; geographical distribution; and embryology; in so far as the knowledge of his time permitted. In every one of these fields, except perhaps the broader principles of plant distribution, the

subsequent advances have been enormous. Many new sciences, such as cytology, bio-chemistry and ecology, have come into existence, and have made possible an insight into organic structure, constitution and relationship which was undreamed of even half a century ago.

Just as it is rash to attempt to interpret heredity and variation without a knowledge of the microscopic details of cell and nuclear structure or the physiology of hormones, chalones and enzymes; so it is equally unsafe to explain many questions of distribution without an intimate knowledge of the ecology and physiology of the organisms concerned. The burden of knowledge laid upon the modern evolutionist is thus so great that no one measures up to the possibilities, and it becomes necessary for the worker in one field to obtain second-hand his knowledge of the results in other fields. But it is none the less incumbent upon him to utilize these results intelligently if evolutionary science is to advance.

This is particularly true of such disciplines as the experimental study of heredity and the investigation of cell and nuclear structure, which had their historical origin in complete independence of each other and have since converged so closely that their results are mutually interwoven. Rarely in the history of science has such a remarkable convergence taken place. Modern genetics represents a synthesis of these two sciences into one. Many genera of plants and animals have now been attacked from both aspects, that of breeding experiments and that of cell structure, with mutually beneficial results; and it is too obvious to need pointing out that the present position of genetics, both in our knowledge of heredity and of variation, could not possibly have been attained without such combined studies. *Œnothera* and *Drosophila* are conspicuous examples but there are many others in the recent literature. In future these two sciences cannot afford to stand alone, but must derive mutual support from each other. Interpretations of breeding results, especially those introducing new complications, which ignore or run counter to well known cytological facts, will have little chance of acceptance. Cytology in its turn will greatly benefit by more comparative studies of related races and species, such as are now being made in a number of plant and animal forms. In such way it is to be expected that a synthetic understanding of genetic phenomena from the combined structural and functional or physiological aspects may be attained.

CHAPTER II.

Foundations of the Mutation Concept.

In later chapters we shall deal with the occurrence of mutations in a wide range of wild plants and animals. The writer's book on mutation[1], dealt particularly with the mutations of *Œnothera* and the conclusions to be drawn from them. A cell theory of mutations was formulated, based on the cytological and breeding work with *Œnothera* and incidently a wide range of other forms; and concepts were developed which proved applicable to many other plants and animals. This has involved certain departures from the theory of mutations as originally propounded by de Vries. Instead of the purely hypothetical and conceptual pangens, whose alterations were the putative cause of mutations, it has been possible to link up many of the changes in *Œnothera* with visible structural changes in the chromatin of the cell.

Let us consider for a moment the simplest case of this kind. It is already well-known, but requires restatement because some writers have endeavoured to deny the significance of the facts. The *lata* mutation is now known to occur in *Œ. lamarckiana*, *Œ. biennis* and *Œ. suaveolens*. The peculiarities are the same in every case—obtuse-tipped, deeply crinkled leaves, a somewhat weak or irregular habit of growth, stout rounded buds, almost completely sterile anthers, and 15 chromosomes in the nuclei. This constellation of characters is super-imposed on, or rather substituted for, the characters of the species in each case, and the same mutation has also been observed from some of the mutants of *Œ. lamarckiana* and also in various hybrids. Thus *Œ. biennis* mut. *lata* has small flowers while *Œ. lamarckiana* mut. *lata* has large flowers, but the *lata* forms otherwise agree. *Œ. lata rubricalyx*, two of which occurred in the F_2 of *rubricalyx* × *grandiflora* had *lata* peculiarities combined with the red pigmentation of *rubricalyx*.[2] It is also significant that *lata* mutants sometimes occur in pairs.

Only one hypothesis based on observation has been suggested to account for the origin of *lata* with its 15 chromosomes. In 1908 occasional irregular reduction divisions in the pollen mother cells were observed in *Œ.* mut. *rubrinervis* whereby an 8-6 separation of chromosomes took place in the heterotypic mitosis. This would lead to the formation of two pollen grains with 8

[1] Gates, 1915. [2] Gates, 1914; Gates and Thomas, 1914.

chromosomes and two with only 6. The same irregularity has since been seen in various other types. There can be no reasonable doubt that *lata* originates in this way, through the union of a germ cell having 8 with one having 7 chromosomes, unless we deny some of the best established facts in cytology. Stomps, however (1916), goes so far as to deny the probability of this hypothesis, although he does not venture to offer anything in its place. His denial is based on the fact that several mutant types are known to have 15 chromosomes. But, as has been pointed out,[1] if the 7 gametophyte chromosomes are unlike, as is probable from many general cytological considerations, then 7 distinct types with 15 chromosomes are to be anticipated. Up to the present, no such number of forms having 15 chromosomes has been described from any strain of *Œnothera*, nor have seven such forms been authenticated altogether, although there is no obvious reason why they should not ultimately be found.

The evidence, then, is clear and definite that *lata* originated through a chromosome entering the wrong nucleus in the reduction division. In this way two pollen grains, or one megaspore will be produced, each having 8 chromosomes in its nucleus. The presence of the extra chromosome, as a duplicate of one, will no doubt immediately have its effect on the cytoplasm of the pollen grain or megaspore containing it. So that the mutation must quickly become a property of the cell as a whole, and, theoretically, at least, this will alter the character of the whole male or female gametophyte derived from a spore with 8 chromosomes, though the differences may not always be demonstrable by the microscope. Renner (1919) has shown that visible differences exist between the pollen grains and male gametophytes of various species, and that segregation of these characters takes place in the pollen of the F_1 hybrids. If an egg from a mutated megaspore has 8 chromosomes, it is already different both in nucleus and cytoplasm from an ordinary egg of the type, since the extra chromosome has been producing its effect thoughout all stages of the embryo-sac formation. Nevertheless, the only original change which it is necessary to assume, to account for the appearance of *lata*, is a chance irregularity in which both members of a pair of chromosomes enter the same nucleus in the reduction division. To endeavour to explain the origin of *Œ. lata* through an alteration in a hypothetical pangen when the visible facts of the chromosome structure are so clear, is to desert science for obscurantism.

[1] Gates, 1915, p. 181.

The same irregularity has been observed in animal spermatogenesis and found to produce individuals with one or more extra chromosomes, *e.g.*, in *Metapodius* (Wilson 1909), where the Y chromosome may be represented as many as 6 times in the cells of certain individuals. The most striking case in animals is known as non-disjunction in *Drosophila melanogaster*, where it has been studied by Bridges (1916) in great detail. This consists in duplication of the X or Y chromosomes through both passing to one cell in spermatogenesis, and it leads to the production of individuals whose heredity behaviour, as in *Œ. lata*, is peculiar owing to the presence of these extra chromosomes. It also results in the formation of certain non-viable and sterile types. The whole situation, though very intricate, is perfectly clear, and the chromosome behaviour corresponds with that previously described in *Œ. lata*. Any sceptic cannot do better than study conscientiously this excellent paper of Bridges. No one who studies this subject with any attempt at an impartial frame of mind can fail to agree that the chromosome content of the various individuals determines the differences in their hereditary behaviour. Indeed, it is not too much to say that most of the arguments against a chromosome basis of heredity are based on sheer unfamiliarity with the enormous advances in this subject which have taken place in recent years.

It must not be inferred from the preceding remark that the whole mystery of heredity is believed to have been solved. Such a conclusion would be contrary to the history of every branch of science. It is recognized that no "explanation" is final, but that each discovery represents a further step in analysis, whether it be in the processes of inheritance or in the structure of an atom. The evidence for the independent identity of chromosomes is at the very least equal to that for the existence of electrons, emanations and other particles constituting the atom. Fortunately, physicists are not worried by the argument that until the exact nature of electrons and corpuscles is known it is unsafe to recognize their existence in formulating a hypothesis of atomic structure. But this is the type of argument with which the cytologist is frequently confronted, coming from biologists whose knowledge often does not extend to the chromosomes. The chromosomes are structural facts whose existence can no longer be ignored in any fundamental analysis or interpretation of the structure, development, inheritance or other properties of organisms.

Just as the cell theory of organic structure has long since passed into the realm of fact, so in a sense has the chromosome theory of inheritance. We need mention only three of the most striking cases where a definite relationship has been established between a particular chromosome complex and a certain set of external characters. These are (*a*) the sex chromosomes, now known to show dimorphism in a wide range of animals, and recently discovered in a liverwort (Allen 1919); (*b*) the aberrant chromosome conditions in the *Œnothera lata* series of forms; and (*c*) the non-disjunction phenomena in *Drosophila*. In all these cases, without obscuring the issues by introducing the concept of "causality," it is definitely known that a certain set of external features of the organism is associated with a certain structural complex of its nuclei, and this complex has been passed on by mitotic division from its inception in the fertilized egg. This is not hypothesis but fact. *Œnothera lata* whenever it is examined (some 50 individuals have had their chromosomes counted) invariably shows the extra chromosome in its mitotic figures. The spermatocytes or the embryonic tissue of the males in various groups of insects show the characteristic male constellation of chromosomes, *i.e.*, with an X or an XY group in addition to the autosomes, while the females show a corresponding XX group.

While we must therefore regard the "chromosome theory," like the cell theory, as an established fact up to a certain point, so, again like the cell theory, must we also regard it as subject to qualifications and limitations.

Since we are not here discussing the general arguments for a more minute and detailed relationship between the chromatin and the complex of inherited characters, this aspect of the subject may be left for the present, with the remark that in the three classes of cases cited a definite relationship which may be classed as hereditary has been clearly established between particular external features and particular chromosome complexes of the nuclei.

(To be continued).

CAMPYLONEMA LAHORENSE, A NEW MEMBER OF SCYTONEMACEÆ.

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[With Six Figures in the Text.]

In Lahore in the month of August during the rains, a very beautiful blue-green alga makes its appearance on lawns and waste grounds where water stands for a day or two and then slowly dries up. In damp places thus left after the evaporation of water, small, shiny, bluish-green, circular patches are seen amongst tufts of grass. These slowly extend on all sides and become irregular in outline till finally they run into one another and produce a very wide, woolly, bright bluish-green stratum on the surface of the damp soil. As the soil dries the stratum takes on a brownish tinge till finally when it is quite dry it becomes dark-brown. A healthily growing vegetative stratum is partly embedded in the mud and is partly above it (Fig. 1). In the subterranean part the filaments

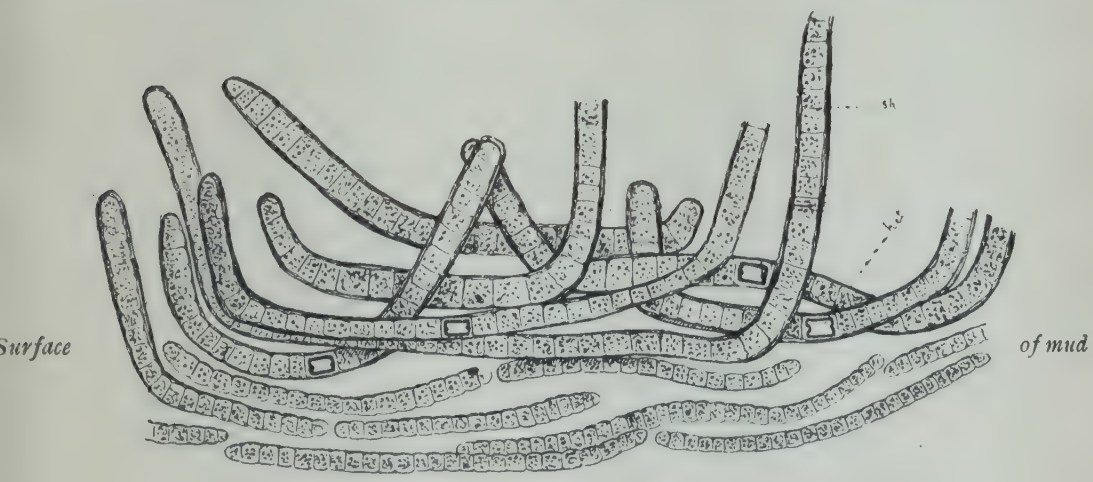

Fig. 1. A small portion of the thallus, showing the filaments in its embedded and aerial portions. *sh* sheath, *het* heterocyst × 286.

are straight, of lighter colour, run more or less parallel to one another and have no distinct sheaths. Those near the surface of the soil are generally curved in the middle and have the two ends abruptly ascending into vertical aerial arms. Each of these exposed arms is enclosed in a sheath, which is thin and hyaline at first, but which later on becomes thick and lamellose, and brown or yellowish-brown in colour (Fig. 2). As the soil dries the sheaths extend towards the middle of the filament and might finally meet so as to enclose the whole of it.

The filament. The filaments measure up to one and a quarter m.m. in length, the matureones being curved in a more or less semi-circular manner. Occasionally pseudo-branches are given off, either singly at the base of an heterocyst (Fig. 3) as in *Tolypothrix*, or rarely in pairs—generally in old filaments—between two heterocysts (Fig. 4) as in *Scytonema*. Trichomes 6-9μ thick, bluish-green, slightly constricted at the joints. Cells 5-11μ long, with coarsely granular contents. Dissepiments are generally not very distinct in mature filaments, but are easily seen in hormogones or young filaments.

The sheath. The sheath is at first thin and hyaline, but later on becomes thick, often lamellose and yellowish-brown, up to one micromillimeter thick. It is very inconspicuous in filaments or portions of filaments embedded in mud, but in exposed filaments or parts of filaments it is brown, firm, thick and tightly adhering.

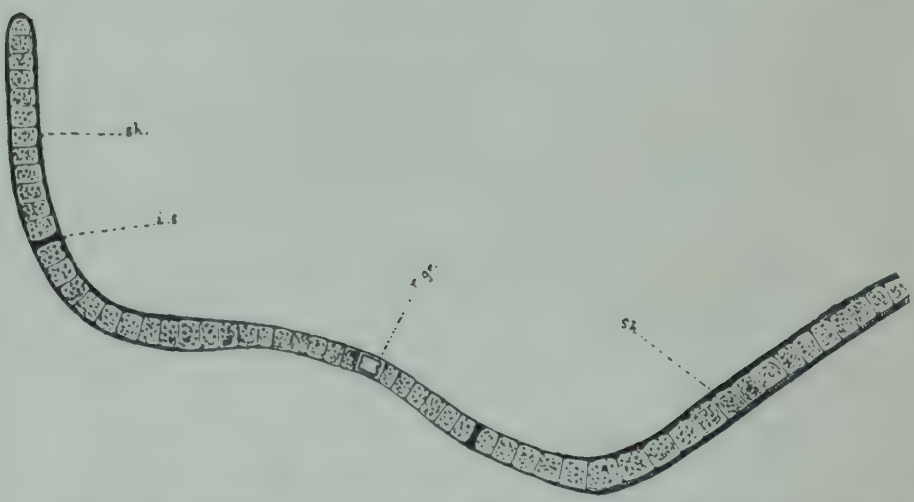

Fig. 2. A typical filament showing the incomplete sheath, median heterocyst, and inter-cellular substance. (*i.s.*) *r.g.* refractive granules × 286.

Heterocysts. One heterocyst is, as a rule, found in the middle of the filament (Fig. 2). Sometimes, however, two heterocysts are found side by side at this place (Fig. 5). Other heterocysts are situated at intervals through the whole length of the filament (Fig. 3). The heterocysts are at first pale yellow in colour and have some finely granular contents. Later on they lose these contents and become hyaline. The refractive granules situated adjacent to the pores at each pole, as mentioned by West (4) and Fritsch (1), are quite easily seen in most cases (Fig. 2). The heterocysts are 12-21μ long, 7-9μ broad, and rectangular or ellipsoid in shape.

Perennation and Multiplication. In unfavourable conditions such as drought, as a rule, the filaments lie enclosed in their thick sheaths, thus giving the stratum a dark-brown colour. They are very fragile in this condition. When the favourable conditions recur, trichomes, generally broken up into a number of hormogones, slowly come out of the sheaths and lie more or less parallel to one another, thus forming a fresh bluish-green stratum. These hormogones may consist of even one or two cells. They resemble the filaments of *Oscillatoria* in general appearance and may be easily mistaken for the latter. They are produced generally by the secretion of an inter-cellular substance or sometimes by the death of vegetative cells here and there. The inter-cellular substance is dark-green in colour and is in the form of a biconcave disc (Fig. 2).

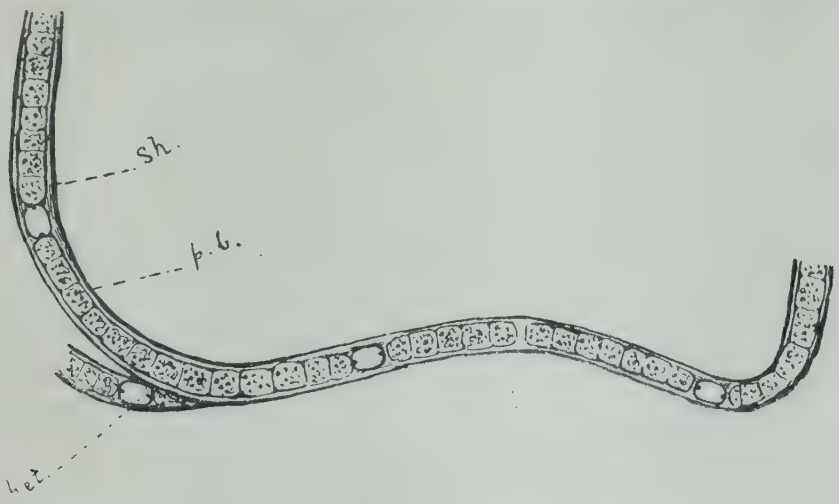

Fig. 3. A filament showing many heterocysts *(het.)*, and a single pseudo-branch *(p.b.)*, at the base of one of them. (× 450).

Rarely spores were seen forming a chain inside the sheath. The sheath in these cases was found to be thin and smooth, though firm and brown (Fig. 6). Each spore has a thick smooth outer membrane and a very thin inner membrane. It is about 8μ long and about 6μ broad and has homogeneous or very finely granular contents. The ejection and germination of these spores have not yet been seen by the writer.

Systematic. The alga described above, although to some extent it resembles *Tolypothrix arenophila* W. and G. S. West, and was to that species by the writer in a former paper (2), shows many characters which render it hardly possible of reference even to the genus *Tolypothrix*. Firstly, heterocysts are frequently found at intervals during the whole length of the filament as in *Scytonema*, and are seldom confined to the base of a

pseudo-branch as in *Tolypothrix*. Secondly pseudo-branches themselves are very rare, and as a rule, filaments are unbranched, though having one or more heterocysts. Even when pseudo-branches are present they are given off singly or in pairs as has been mentioned above, thus partaking of the characters of both *Tolypothrix* and *Scytonema*. A third characteristic is the curved shape of the filament.

Fig. 4. An old filament showing the thick sheath and paired pseudo-branches. (× 450).

The genus *Campylonema* was monographed by Schmidle in 1900 (3) to include members of the Scytonemaceæ with generic characters resembling those of the alga described above, with the exception that no mention of the presence of spores was made. Only one species, *C. indicum* Schm. has been described from Bombay, from which the alga under discussion differs in many respects. It is not epiphytic on Hepaticæ like *C. indicum*, but occurs on damp soil forming a vast stratum. The thallus is thin and woolly and not fasciculate and crisp as in *C. indicum*. Trichomes are not very torulose and ramose upwards as those of *C. indicum*, and are not so thick as the latter.

For the above reasons I propose to refer the alga described in this paper to the genus *Campylonema* and to create a new species,

Campylonema Lahorense with the following specific characters:— Thallus woolly, bright bluish-green or bluish-brown, terrestrial, partly embedded in mud and partly above it; sheath inconspicuous, thin and hyaline in the embedded portion, and firm, thick, lamellose, tightly adhering, and brown in the exposed portion; filaments curved in a more or less semi-circular manner, up to $1\frac{1}{4}$ mm. in length; trichomes bluish-green, 6-9μ in diameter, slightly constricted at the joints, rarely pseudo-branched, pseudo-branches given off singly or in pairs; cells isodiametric or a little longer or shorter than the diameter; transverse walls scarcely conspicuous in older filaments; heterocysts median or found at intervals

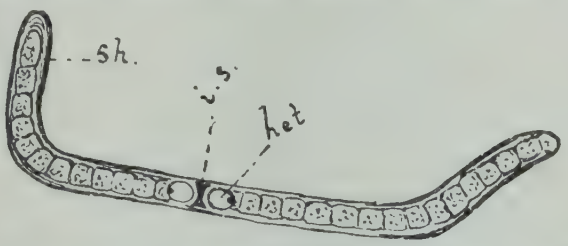

Fig. 5. A filament showing two median heterocysts. (× 400).

through the whole length of the filament, rectangular or ellipsoid, 12-21μ long and 7-9μ broad; spores 7-11μ long and 5-7μ wide, formed in a chain within the sheath, with brown thick and smooth episporium; cell-contents coarsely granular.

Habitat:—On damp lawns and waste grounds at Lahore, India.

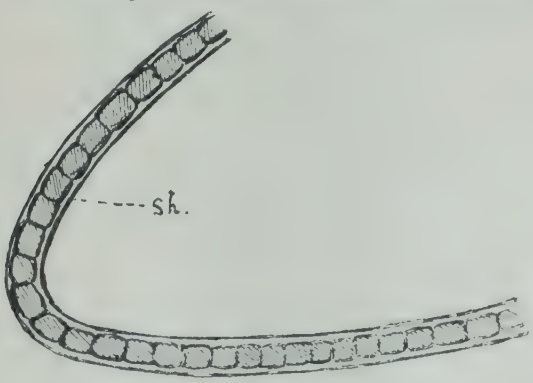

Fig. 6. A filament forming a chain of spores. (× 450).

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THE OCCURRENCE OF ACTINOMYCES-LIKE ENDOTROPHIC MYCORHIZA.

By Jean Dufrenoy.

(*Assistant, Biological Station, Arcachon, France*).

[With Five Text Figs.].

I.—*Mycorhiza in Adenostyles albifrons.*

1. *Ecology.* Small well defined patches of *A. albifrons* occur in the Beech woods of the Pyrénées, near Barèges, at heights of about 3700 feet. The vertical shoots bear leaves, heavily rusted by *Uromyces cacaliæ* and much fed on by *Chrysomela gloriosa*. Long fleshy rhizomes run horizontally, giving long horizontal roots, rich in trichomes for most of their length. Both rhizomes and roots trail in the superficial layer of *undecayed*, fallen leaves, so that the plant is very easily uprooted.

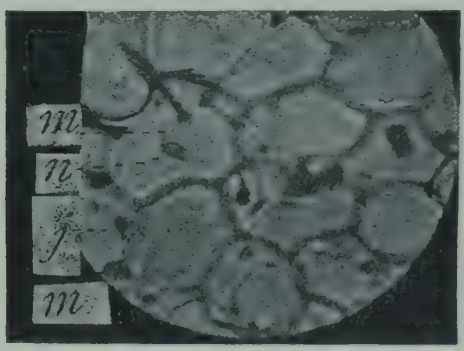

Fig. 1. Root of *Adenostyles albifrons*, transverse section, stained with carbolic crystal violet, then treated with I+KI. *m.* massue, gram positive. *n.* nucleus, within a net of hyphæ (not coloured) and their club-shaped "massues." *J.* nucleus of a non infected plamolysed cell. (Photomicr., oil imm. $\frac{1}{15}$ obj. Oc. 1., Stiassnie).

2. *The Endotroph.* Many hyphæ coil around the trichomes, and some of them push through the gelatinous pectic walls of the epidermal cells into the inner parenchymatous cells of the cortex, and even into the vascular system, the pericyclic tissues being heavily infected. Hyphæ show nearly as well in the cortex of the *rhizomes;* they were not observed in the petioles.

3. *Cytology of infection.* Roots were fixed in Bouin's picro-formol and hand-sectioned. Hyphæ were directly demonstrable by clearing with lactophenol, or staining with cotton-blue. But it is best to stain with carbolic crystal-violet, then to differentiate with amyl-alcohol, which stains the endotroph a deep blue, while the host-tissues display a light metachromatic rose-colour.

Hyphæ growing into some of the parenchymatous cells form a network round nucleus; locally they swell into little club-shaped masses ("massues"). These are either directly inserted on the hyphæ, or (as may occur in the rhizomes), terminate short lateral branches (Fig. 5, ct).

The hyphæ are acid fast and retain a red colour after coloration by carbol fuchsin and the Ziehl-Niellsen method. The "massues" are basophilous—and more so as they age; they are "gram positive," and stain a deep blue with cotton blue.

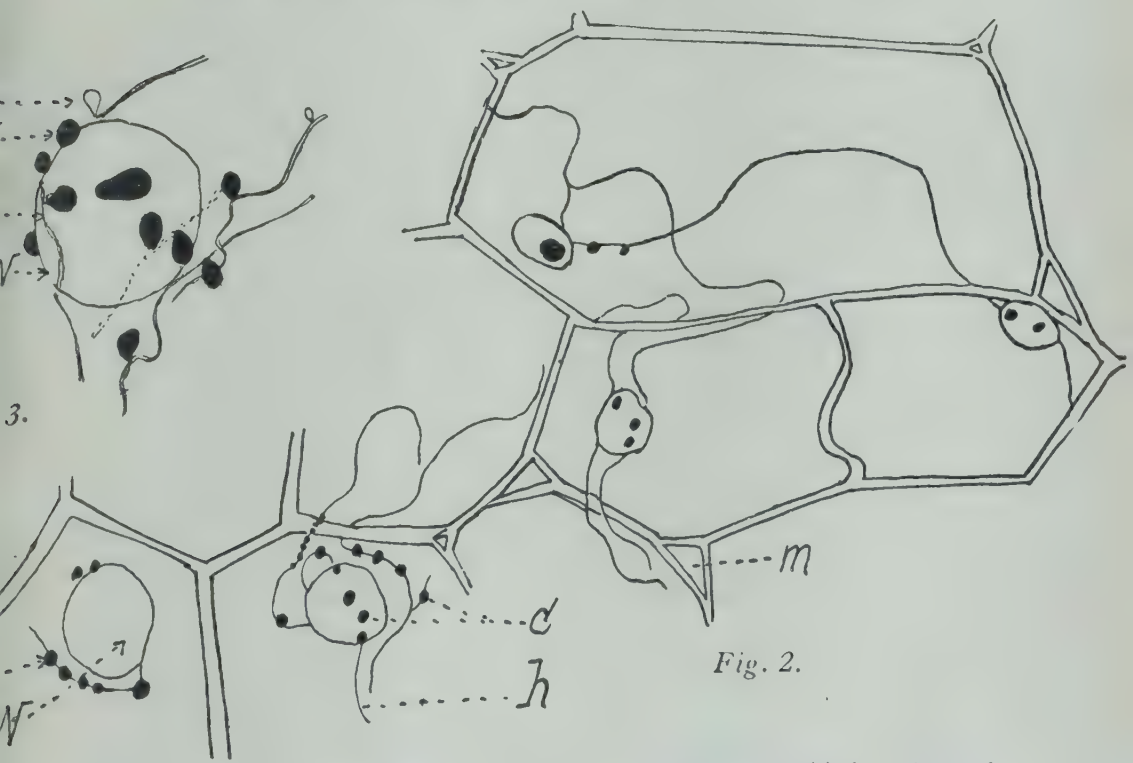

Fig. 2.

FIG. 2. From same section as FIG. 1. *N.* Hypertrophied nucleus of parenchymatous cell. *c.* club shaped "massues." *h.* hyphæ (uncoloured by alcohol).

FIG. 3. Nucleus of infected cell, showing detail of infection and relative dimensions of endotroph. (Oil imm. obj. $\frac{1}{15}$, oc. 9).
N. Nucleus, *c*, full grown "massues," (gram-positive) *d*, young "massue," *h*, hyphæ.

The nucleus in infected cells enlarges or may divide; the nucleolus becomes larger and basophilous. The whole of the nuclear material becomes granular and retains basic dyes, whereas the nuclei of the epidermal cells are acidophilous and stain deeply with eosine.

No hypertrophy of infected cells was observed, but hyperplasia may result from division by irregularly placed walls. Cytoplasm may shrink in neighbouring non-infected cells, which brings the nucleus into contact with the cell wall (Fig. 1).

II.—*The significance of "massues" in parasitic Actinomyces.*

Contrary to what we observe in the endotroph, the ordinary *Actinomyces* of "Actinomycosis" has acid-fast "massues" and basophilous hyphæ (1). Still we consider the club-shaped swellings in *Adenostyles albifrons* to have the significance of "massues" and therefore place this endotroph in the genus *Actinomyces*. Similar swelling-forming Endotroph has been reported by Peklo and Arzberger from the tubers of *Myrica gale*, and ascribed to an

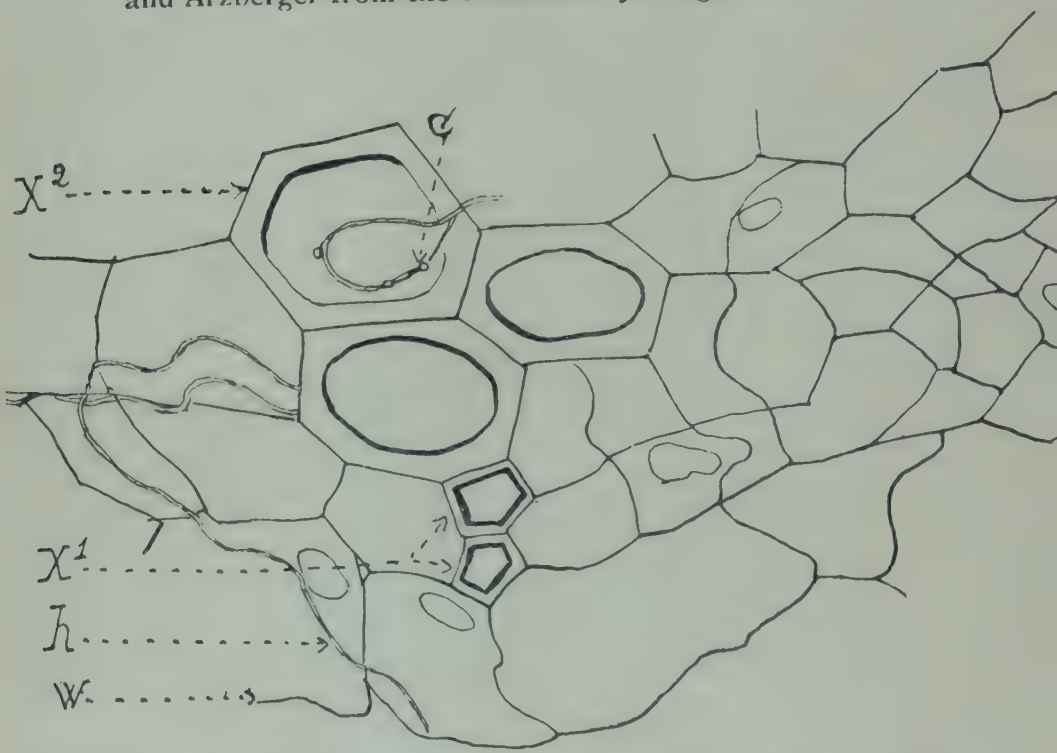

Fig. 4. Inner cortex and vascular tissues of root, coloured by the Ziehl-Nielssen method.

*X*1 protoxylem, *X*2 metaxylem, *w*, cell wall, *h*, hyphæ (about 2μ in diameter) *c*, "massues" (uncoloured by action of HNO_3).

Actinomyces, without any cytological evidence being adduced to enforce this conclusion (2). "Massues" indeed may be considered characteristic of *Actinomyces* growing in their infected hosts; they have also been recently reported from cultures submitted to the action of high temperatures or of various salts.

III.—*Conclusions.*

Actinomyces may be held responsible for two cases of endotrophic mycorhiza. This conclusion, however, being largely speculative demands for further investigation of the cases and also a precise definition of the genus *Actinomyces* (3).

Infection *of the shoot* by endotrophs occurs in Compositæ as well as in Orchidaceæ and Ericaceæ (4, 5, 6).

FIG. 5. Rhizome of *A. albifrons*. Section of Cortex, coloured with Cotton blue (Oil imm. obj. $\frac{1}{15}$, oc. I). *ct.* terminal (acrogenous) "massue"; *N*, nucleus; *K*, granular nucleus; *h*, hyphæ.

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THERMAL LABORATORY, BARÈGES, 1919.

ELEMENTARY LECTURING WITH THE HELP OF SCHEDULES.

ELEMENTARY NOTES ON STRUCTURAL BOTANY, by A. H. CHURCH (12 lectures), Oxford Botanical Memoirs, No. 4., Oxford Univ. Press, 1919. Price 2s. net.

ELEMENTARY NOTES ON THE REPRODUCTION OF ANGIOSPERMS, by A. H. CHURCH (10 lectures), *Ibid*, No. 5., 1919. Price 2s. net.

THE method of teaching science by means of formal lectures followed by practical work in the laboratory, leaves much to be desired, especially in the case of elementary students. The fundamental criticism of this method from the standpoint of educational psychology is of course that the student is put into a passive and receptive instead of an active, critical, and executive frame of mind. He sits still and has information poured into him, and the active working of his own mind, without which real education is impossible, is apt to be at a minimum. And this unfortunate attitude, which is more or less forced on the student by the method of instruction in the lecture room, is only partially bettered by the cutting, inspection and drawing of sections which still forms the mainstay of the laboratory régime. Nevertheless the practical convenience of the method, especially to the teacher, is so great, that it still maintains itself in full vigour.

We are not concerned, at the moment, with suggesting alternatives, or with trying to determine the legitimate function of the lecture in teaching. But accepting the lecture system as an integral part of the method of instruction, it is clear that if the student takes his primary information solely or mainly from the lips of his lecturers, and records or tries to record what he hears in his notebook, he runs a grave risk both of failing to get his information accurate and of missing a large part of the real value of *vivâ voce* teaching. There's many a slip 'twixt the lecturer and the notebook, defective hearing, defective mechanism in the process of translating what is heard into what is written, slips in writing, and finally the failure to record what the lecturer says from lack of time. Any lecturer may convince himself that these failures of mechanism are very real by the simple process of inspecting his students' notebooks. As a method of communicating information the lecture is indeed largely a relic of mediævalism, of a time before the printing press made possible the accurate multiplication of copies of what a man has to impart.

All these considerations are of course the merest commonplaces to professional educationists, but they are very generally neglected by university teachers. Mr. Church, in his elementary teaching at Oxford, has adopted a method by which the defects of the ordinary lecture are largely overcome. The method is not new—the writer himself used it with success in one of the first elementary courses he ever gave, a great many years ago : it is to some extent embodied in all lecture courses of which a fairly full syllabus is issued ; and for all we know it may be used extensively in the colleges and universities of the country. The method is simply to write down the substance of the lecture—the leading facts and ideas—in a condensed form, and to distribute copies, printed or otherwise multiplied, to the members of the class. Thus the student has, and knows that he has, the substance of what he would otherwise have to try to write down in his notebook, *in an accurate and authoritative form.* He is therefore free to *attend* to the lecture *with his whole mind*, being relieved from the strain of trying to get down as much as he can, and thus from the necessity of *attending*, not to what the lecturer is saying, but to what he said several seconds before. He can sit back and appreciate the lecture as a whole, get the whole thing into perspective, allow the light and shade, the varying emphasis, to make its full impression. Mr. Church expresses the difference by saying that whereas he used to lecture to a row of heads, with their attached hands writing for dear life, he now addresses a set of human beings listening to what he has to say. The only possible disadvantage of the method is that it enables the incorrigibly lazy student to be a little lazier, to leave his mind a blank or let it wander through the entire discourse. But it is doubtful if such students can be perceptibly benefited by any system of lecturing as such.

Secure in the knowledge that his class possesses copies of the main substance of his topic, the lecturer need not keep closely to the printed text. He may, if he chooses, elaborate special points, discuss further illustrations, develop side lines, or what not. He is no longer bound to plod laboriously through his basal data, for those are recorded in the leaflets. The printing press takes over the mechanical function of imparting cut and dried data, and both the lecturer and the class are free to enjoy the real irreplaceable advantages of *vivâ voce* teaching—the influence of the living personality of the teacher and the power of varying emphasis.

Each of Mr. Church's leaflets contains about 1400 words—as much as, or more than, a good elementary student could get down in his notebook in the course of an hour's lecture. Towards the end of the leaflet the material used in the practical work is introduced. The whole forms a condensed text-book representing twenty-two lectures, covering "two-thirds of the general elementary syllabus for the Preliminary Examination in Botany of the School of Natural Science" at Oxford, "a set on 'Lower Types' being required to complete the evolutionary scheme." We do not propose to criticise or comment on the actual contents of the leaflets, beyond making the remark that while doubtless no one will or should want to follow exactly the scheme of another teacher, these notes will be found intelligent, thorough and suggestive. We think Mr. Church has rendered a real service to university teachers by publishing his "Notes" and we commend them heartily to our readers.

One more point may be mentioned. There is a good deal to be said for issuing the notes of the entire course at the commencement, or, if the leaflets are issued separately, to give out each at the lecture before the one at which the corresponding topics are discussed. In this way the keener students can make themselves familiar with the skeleton of the lecture before it is delivered, and the lecturer can, in the case of small or moderate sized classes, ask questions on the substance of the schedule, and use the answers as a text for further explanation.

A. G. T.

JAMES WILLIAM HELENUS TRAIL, M.A., M.D., F.R.S., F.L.S.

JAMES W. H. TRAIL was born at Birsay, Orkney, in March, 1851. At the age of eleven, he was sent to school in Aberdeen, and some years later, on the appointment of his father to the Chair of Systematic Theology at Aberdeen University, that city became the permanent residence of the family, which thus returned to the region from which it had sprung.

The boy rather reluctantly went through the classical curriculum at school and college which was demanded by the tradition of his family and of his University alike. From an early

age his mind turned to natural history, and while a student he arranged and added to the collection of insects in the University Museum. His bent was not encouraged, but when he had completed his arts course, he was permitted to proceed to the study of medicine. Fired by the works of the early explorers of tropical South America, he hoped that an appointment as doctor to some expedition in that region would give him the opportunity of definitely adopting a scientific career. This hope was exceeded when in 1873 he went to Brazil as botanist to the Amazon Steam Navigation Company, and there spent two years in exploring the tributaries of the Amazon. In 1876 he accepted the post of botanist to the Colony of British Guiana, but in 1877, before he had sailed, he was appointed Regius Professor of Botany at Aberdeen University, succeeding George Dickie as the second occupant of the Chair. He was elected a Fellow of the Royal Society in 1893, and was President of Section K of the British Association in 1911. At his death after a short illness on the 18th of September, 1919, he was senior member of the Senatus of the University, with forty-two years' service.

Professor Trail's scientific work began with his papers on the Palms of Brazil in the *Journal of Botany* 1876-7, and was continued by a long series of contributions to the natural history of Scotland in the *Annals of Scottish Natural History*. In recent years he was most interested in the changes occurring in the native and introduced flora. He believed that these could best be traced and explained by the compilation and comparison of exact records of distribution, and devoted his energies to the task of amassing the necessary data. The material thus collected forms an invaluable record of the present distribution of the flowering plants, of the plant-galls, and of certain groups of fungi in Scotland. Carried to the finest point, his methods resulted in a study of the flora of the City Parish of Aberdeen, which will be published by the Aberdeen Natural History and Antiquarian Association. In it, the changes, mainly due to the influence of man, are minutely traced from the time of the earliest records. A collector of insects in his youth, he remained a keen entomologist with a wide knowledge of British forms. The galls formed a link between his two interests. All his work was permeated by the spirit of the early naturalists, which found its satisfaction in the observation of living things in the field.

The journey to South America coloured his whole outlook, and this was seen especially in his teaching. For illustrations of

the facts of biology and external morphology, on which he laid most stress in his lectures, he drew largely on his tropical experience. Many a doctor and teacher must look back on the Botany Class as a strenuous time. The lectures were held at 8 a.m., and evening and Saturday excursions were a prominent feature of the course. It was as necessary to be a good walker as a good observer, for the Professor's stride was long, and covered much ground in little time. The excursions were perhaps the most valuable part of his teaching; they permitted the free expression of his unequalled knowledge of plant life. A running commentary, to his immediate following, on the ways of plants and animals seen was interrupted only to name the plants brought to him. The reiterated warning that "scraps" were of no use was negatived by an unfailing identification of the most fragmentary specimen. His skill in "running down" plants of all classes was appreciated and made use of by a large circle of friends, acquaintances, and strangers; his help was extended to every applicant.

His students could always count on advice and assistance, and his kindly attitude has encouraged many to become scientists. Most have followed the lines he himself favoured and are occupied in systematic and economic work in our tropical dependencies and our museums. But his support was extended with equal warmth to those whose interests lay in other fields. Assistance took a generous and very practical form in the foundation of several University endowments.

Besides occupying the Chair of Botany he was Lecturer in Agricultural Botany to the North of Scotland Agricultural College, and his administrative activities were very numerous.

Professor Bower has termed him a "typical Aberdonian." Perhaps in that county the quality emphasised in Charles Darwin's motto is even more highly developed than in Britain as a whole. In the early tenacity with which he pursued his intention of being a scientist, no less than in the persistence with which he later carried on his investigations, Professor Trail showed that he too believed "It's dogged does it." M. S.

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A THEORY OF GEOTROPISM:

WITH SOME EXPERIMENTS ON THE CHEMICAL REVERSAL OF GEOTROPIC RESPONSE IN STEM AND ROOT.

BY JAMES SMALL, D.SC. (LOND.)

Professor of Botany, Queen's University, Belfast.

[WITH PLATE I AND FIVE FIGURES IN THE TEXT.]

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CERTAIN theoretical considerations have led to the conclusion that the difference in the responses of the stem and the root under the stimulus of gravity depends upon the relative[1] alkalinity of the continuous phase of the plasma membranes of the stem apex and the relative acidity[1] of the corresponding medium in the root apex.

The experimental evidence for this view and the theoretical considerations involved, form the substance of the present contribution.

[1] "Relative," that is, to the isoelectric point of the protein or other particles of the disperse phase of the plasma membrane.

Preliminary Theories.

In an endeavour to find an explanation of the difference in the increase of electrical conductivity shown by the upper and under sides of a horizontally placed root (18-19), certain hypotheses were used. These included as a corollary a preliminary explanation of the difference in the geotropic response of stem and the root.

Hypotheses.

1. The increase in electrical conductivity is due to increased permeability of the protoplasm to ions. This hypothesis is supported by the work of McClendon, Osterhout, Stewart and Waller (see 12, pp. 103, 122), and particularly by that of Clowes (2-3). In spite of the criticism by Stiles (22) of the "assumption" that conductivity is a measure of permeability, this "assumption" is very widely used and very strongly supported by experimental evidence. The work of Höber and others makes it seem probable that "the chief impermeable layer of all cells is the plasma membrane" (12, p. 92). Lillie (11) also states that it has been found that the process of stimulation is always accompanied by an increase in permeability and probably is often dependent upon it.

2. The increased permeability was assumed to give decreased turgor.

3. The protoplasmic layer governing the permeability was assumed to contain rapidly moving (*i.e.*, exhibiting the Brownian movement, cp. Price, 16, p. 602-3) colloidal particles of a protein nature. This layer is probably of a suspensoid structure (*i.e.*, at least partly denatured) rather than of a purely emulsoid character.

The protoplasm was conceived to be an emulsion of protein or protein-lipoid particles in a colloidal protein medium. It has been shown by Fischer (4) and confirmed by Roon and Oesper (17) that a hydrated colloid is an essential part of an emulsion. It has also been shown by Fischer (4) that, while neutral casein is not a good emulsifying agent, alkaline or acid casein emulsify equally well, either becoming the hydrophilic colloid necessary as a dispersing agent.

The permeability was considered to depend on adsorption of the ions and salts by the active particles and not to be a chemical phenomenon as suggested by Stiles (21) nor a more or less static phenomenon as suggested by Fischer [(5-6), and cp. Henderson (10)] and Free (7) and Tolman (23)[1]. It was considered to be kinetic and dynamic.

[1] The views of the last author on the influence of the H-ion concentration and amphoteric colloids are very similar to those outlined below. The differences are those between a spongy structure which would not be affected by gravity and an emulsion which creams under the influence of gravity and centrifugal force. The latter is the structure observed by Price (16).

4. The semi-permeable membrane was assumed to be polarised. This is a generally recognised phenomenon (see 12, pp. 106-120).

5. The polarisation was assumed to be due, in part at least, to the electric charges on the protein particles (see 12, pp. 123-124). Proteins are known to be amphoteric colloids which are electropositive in acid media and electronegative in alkaline media. But many proteins, such as albumins and globulins, are more acid (electronegative) in themselves than basic; to render such proteins electropositive, requires therefore, a H-ion concentration (or acidity) greater than that of the protein itself.

6. The difference in the geotropic response of stem and root was supposed to be due to a difference in the charges of the protein particles in these two organs. The continuous phase of the plasma membrane in the root was supposed to be acidic beyond the PH of the isoelectric point of the protein or protein-lipoid particles of the disperse phase of the membrane. The corresponding phase of stem plasma membranes was supposed to be of an acidity below the PH of the protein particles, *i.e.*, on the basic side of the isoelectric point of the protein. The particles of the disperse phase of the plasma membranes in the perceptive region of the stem would then be electronegative; while the particles of the disperse phase of the plasma membranes in the perceptive region of the root would be electropositive.[1]

7. "There is abundant evidence to show that the plasma membrane in the resting condition is electrically polarised, and that increase in permeability reduces this polarisation" (12, p. 149). That reduction of the polarisation as such gives an increase in permeability seems probable from many investigations on the effect of acids, alkalies, salts and other substances on the permeability of both plant and animal cells.

Explanation of the Difference between the Upper and Under Sides of a Horizontally Placed Root.

With these hypotheses an explanation is suggested for the differential action of gravity on the upper and under sides of a root when it is placed horizontal. Considering the diagram (Fig. 1) the change in the polarisation of the cells in the perceptive region is supposed to affect each cell to the same extent but in an unequal or one-sided manner, *i.e.*, the amount of the change is the same in

[1] Haas (9) has shown that no acid or acid-forming substance other than CO_2 is excreted by the living root, and it seems probable from preliminary experiments that the CO_2 balance in stem and root is the chief factor governing the differentiation in hydrogen ion concentration.

in each cell but the lower side of the cell becomes differentiated from the upper side. The change is visualised as the "creaming" of the suspensoid protoplasm[1]; the electrically charged particles are supposed to ascend and thus decrease the polarisation of the lower side of the cell, while increasing the polarisation of the upper side of the cell to an equal and opposite extent.

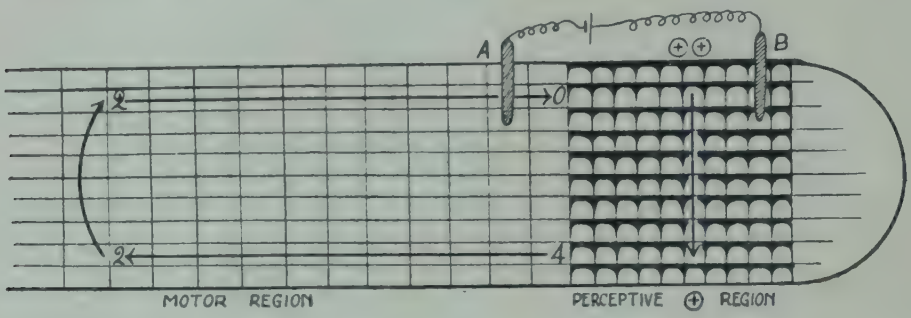


FIG. 1. Diagram of root-apex.

The more highly polarised surfaces are the upper ends of the cells while the lateral surfaces are increasingly polarised from bottom to top. Reduction in polarisation involves increase in permeability and decrease in turgor, and since these are relative terms, increase in polarisation involves decrease in permeability and increase in turgor.

In the erect position the asymmetric polarisation of the cells has no apparent effect because these regions of different polarisation are symmetrically arranged around the axis of the root. Any electric current developed as the result of the potential differences between upper and lower surfaces of the cells must likewise flow symmetrically, either down the centre and up the cortex or up the centre and down the cortex. The longitudinal growth of the root might be explained in this way.

In the horizontal position the asymmetric polarisation of the cells is arranged as in the diagram (Fig. 1). Even single cells are now recognised to be concentration cells with a definite though small electromotive force. This EMF in the normal resting condition is considered to be developed between the negatively charged outer layer and the inside of the cell which has a lower potential. In the root the outer layer was supposed to differ from the normal case in being electropositive instead of electronegative

[1] This "creaming" is dealt with very fully for particles of greater density the medium by Perrin (15). The laws governing the creaming of particles of lesser density than the medium are the same. The perceptive region and motor region differ in the height available for the creaming which is governed by Stoke's Law.

(see hypothesis 6). In the case of the vertical root there would be not only a reversed normal EMF, but a definite EMF developed as a result of the greater positive polarisation of the upper surface of each cell in the perceptive region, giving a difference of potential between the upper and lower ends of the cell. For one cell this EMF would be small, but the cells may be regarded as connected in parallel (laterally) and in series (longitudinally); the EMF would, therefore, be something quite appreciable (several hundred millivolts). The arrangement of these concentration cells and consequently of any current developed is symmetrical about the axis of the *vertical* root and no curvature would be produced.

When the root is placed horizontally the potential differences are no longer arranged symmetrically about the axis of the root. There is a higher potential (because of the "creaming" and greater polarisation) on the upper side of each cell and therefore an EMF is developed which produces a current flowing from the upper side to the lower side of the perceptive region of the root (Fig. 1). This may be described as an "action" current[1] and, on account of the resistance in the circuit, it will produce its maximum effect in the under side of the root.

One effect of the current is naturally the lowering of the polarisation of the cells giving a greater increase in permeability to ions and in conductivity in the under side of the root than in the upper side.

This current is developed in the sensitive, perceptive root apex and may be considered to be the cause of the stimulation of the cells of the motor regions. This electrical stimulation of the cells of the motor region would be, as shown above, greater in the under side; this would produce a greater increase in the permeability of the under side than of the upper side, giving greater relative turgor in the upper side and therefore greater growth of that side. The downward curvature of the root and the decrease in the rate of growth under geotropic stimulation are, therefore, explained, together with the variations in conductivity found.

It should be noted that for the effect to be greatest in the under side the outer surface of the plasma membrane is supposed to be electropositive, because the particles of the disperse phase which produce the polarisation are enclosed by a continuous phase which is acidic beyond the isoelectric point of the protein particles.

[1] Bose (1) has recorded data which prove that potential differences, such as would occur in this case, do exist in the stimulated root and stem.

Explanation of the Upward Curvature of the Stem.

According to hypothesis 6 the protein-lipoid particles of the disperse phase of the plasma membranes in the perceptive region of the stem apex are electronegative (instead of electropositive as in the root) because the continuous phase of the plasma membranes in that region is of an acidity less than that of the proteins concerned. The medium or continuous phase is not necessarily or even probably alkaline, but it is supposed to be on the basic side of the isoelectric point of the proteins and is probably slightly acid.[1]

In the perceptive region of the vertical stem there is the same creaming effect as in the root, giving a symmetrical distribution of polarised areas as in the vertical root, but the polarisation of the upper and lower surfaces of the cells is arranged in the opposite way to that in the root. The upper ends instead of being of a

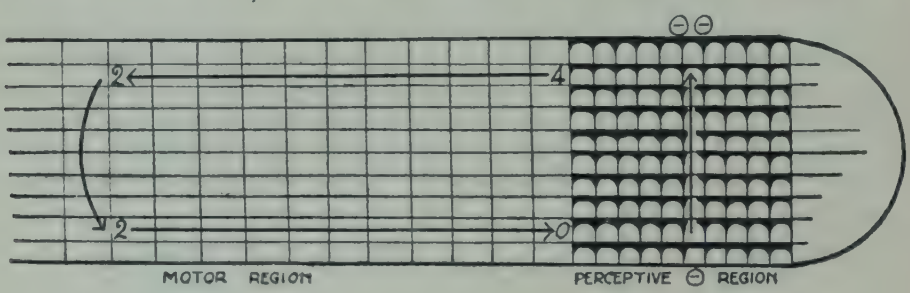


Fig. 2. Diagram of stem-apex.

higher electropositive potential than the lower ends of the cells are of a higher electronegative potential. This gives an arrangement of potential differences which are symmetrical about the axis of the vertical stem, and may at the same time account for some of the polarity of growth shown by the rootless, subaerial cryptogams.

When the stem is placed horizontally these potential differences again cease to be symmetrically arranged about the axis. The potential differences produce an EMF which gives a current from the under to the upper side of the perceptive region (Fig. 2); the direction of the current in the stem is the reverse of that in the root. Resistance is present in the stem as in the root, therefore the greatest effect will be produced in the upper side. The effect of the current on the cells of the motor region will again be an increase in the permeability, which will be greatest in the upper

[1] The H-ion concentration of plant cells as shown by Haas (8) varies in the cases he investigated from PH 3 to PH 8 (PH 7 being the true neutral point), while the PH of proteins as given by McClendon (12, p. 77) varies from 3·52 to 9·3, the majority and especially the plant proteins varying only from PH 4 to PH 5 5. The H-ion concentration of at least some plant proteins is therefore such that the variation actually found in the acidity of plant cells would be sufficient to produce electropositive and electronegative protein particles.

side. The turgor of both upper and under sides of the motor region will, therefore, be reduced, but that of the upper side will be reduced more. Growth will then be greatest on the under side and the stem will curve upwards. The distribution of these electrical effects in the perceptive and motor regions accounts for the fact that, although these two regions may be well defined, there is frequently a curvature which extends from the perceptive region to the comparatively distant region where the chief motor response takes place.

These preliminary theories having been sketched out towards the end of the year 1918, some time was spent in considering which of the many experiments they suggested would be most critical and at the same time convincing; something that could easily be repeated was desired because of certain criticisms of the excessively careful and expert manipulation required for the repetition of the previous experiments (10) on the changes in conductivity under geotropic stimulation.

It was finally decided that, if the reaction of the continuous phase of the plasma membranes in the perceptive region of the stem was really on the basic side of the isoelectric point of the disperse phase, and that of the corresponding medium in the root was really on the acidic side of the isoelectric point, it might be possible to reverse the relations of the reactions of these regions to the isoelectric point. To state the matter in more widely familiar but somewhat misleading terms—taking the isolectric point of the proteins concerned as neutral, the stem growing up because it is of an alkaline nature should grow down if its reaction is changed, while the root growing down because it is of an acid nature should grow up if its reaction is changed. There was, of course, a considerable doubt as to whether the protoplast would continue to function and reversal of the actual curvature was as much as could be expected.

This critical experiment was chosen because it seemed essential to the whole theory to suppose a real difference in the *kind* of charge on the particles of the disperse phase and at the same time an electropositive polarisation of the plasma membrane seemed to be the only point which was at variance with accepted views on the electrical conditions of the cell. These accepted views being based chiefly on animal cells, and no critical experiments having been carried out on the contrasted tissues of stem and root, there was a

possibility of something being added to our knowledge of polarisation in plants. At the same time the experiments seemed to involve no special technique and, if successful, could be repeated by anyone.

Experimental.

The experiments on the problematical reversal of geotropic curvature in stem and root were commenced in May, 1919, and the methods will now be described.

Geotropic Response of the Root.

The primary roots of *Vicia Faba* were studied first. Roots from one to two inches long were used. It was found that excess of ammonia vapour rapidly turned both testa and root quite black; the roots excreted a clear liquid and shrivelled within a day or two. With very dilute ammoniacal water it was found that the vapour was too strong the first day and had all been given off within three days. In order to get a more or less constant supply of ammonia vapour at a low concentration the following procedure was

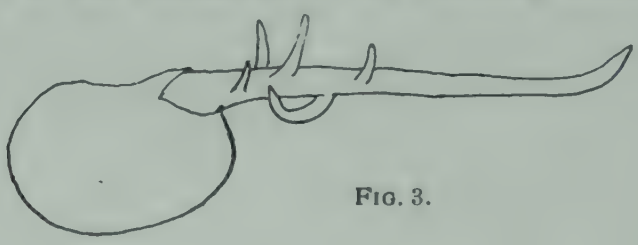
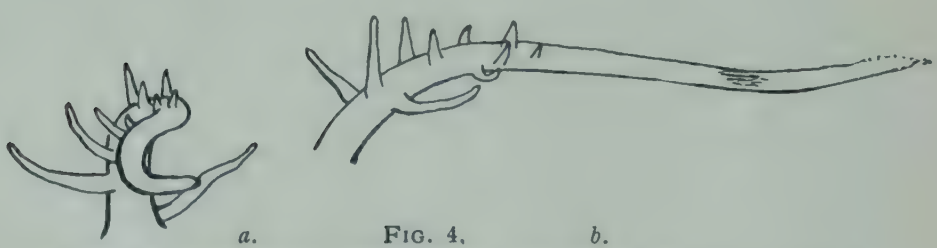


Fig. 3.



a. Fig. 4. *b.*

Figs. 3-4. Secondary roots showing reversed geotropism; Fig. 3, five rootlets; Fig. 4a, ten rootlets, end view; Fig. 4b, ditto, side view.

adopted—a piece of sheet cork was fitted into a flat museum jar so that about one third of the cork was below the level of the liquid filling the jar. The jar was filled with ammonia solution (·880) diluted to 1 in 10 with water. This was placed under a bell jar and allowed to stand for a few days; the ammonia was thus absorbed by the cork. The liquid in the jar was poured off and the jar was refilled with successive lots of tap water at intervals for about a month; the effect of the atmosphere under the bell jar on germinating beans was observed, until the vapour acquired the proper low concentration of ammonia. At this stage the vapour turned red litmus paper blue in about half-an-hour and, although

no smell of ammonia could be detected, a germinating bean pinned to the cork above the liquid had its testa blackened after two days.

With this very slightly alkaline atmosphere various experiments were carried out by pinning the seedlings to the cork above the liquid. In all cases both with *Vicia Faba* and *Zea Mays* controls were grown pinned to cork above a jar of tap water, the whole under a bell jar. These showed the normal responses. The roots in the alkaline atmosphere grew up as shown in figures 1—5, Plate I and Text-Figs. 3-4.

Many more roots were grown in an alkaline atmosphere and while many failed to show the upward curvature, none grew downwards.

These experiments may be taken therefore as preliminary confirmation of hypothesis 6 in so far as the root is concerned. On account of the susceptibility of the plants to alkaline vapour and the growth of fungi after two or three weeks, the experiments with roots were not as satisfactory as those with stems. Direct determinations of the H-ion concentration of the protoplasm of the root apex and stem apex are being attempted, but it should be pointed out that the PH of the sap is not necessarily that of the plasma membrane. The reversal of curvature is considered to be the best test devised at present because in the case of reversed curvature we are dealing with that part of the mechanism which produces normal curvature.

Geotropic Response of the Stem.

In the first stages of experimentation bean seedlings with stems one to two inches long were pinned to cork above water containing about 1% of acetic acid, under a bell jar. No geotropic response was obtained and the stems excreted liquid in the same way as the roots did in an alkaline atmosphere, they afterwards became blackened also but not to the same extent as did the roots.

The best results were obtained with the coleoptile of the maize seedling. The ordinary variety was used for most of the coleoptile experiments, but Sutton's White Horse-tooth variety reacted with equal, if not greater, readiness. The seedlings were grown in moist sand in shallow porous dishes. They were transferred to the cork when the coleoptile was about an inch long and before the first leaf emerged. Controls were grown above tap water, and acetic acid was used as before to obtain an acid atmosphere. It was found that the concentration of the acid could be varied within wide limits and an atmosphere distinctly acid to litmus paper was easily

obtained. Proceeding as before a number of experiments were carried out, with the result that the stems grew down in the acid atmosphere as shown in Figs. 6, 8 to 11, Plate I.

These experiments may be taken, therefore, as further preliminary confirmation of hypothesis 6 in so far as the stem or coleoptile is concerned. The stem has proved to be more satisfactory in the readiness with which it responds to an acid atmosphere, and because fungi do not grow so rapidly under such conditions. It is obvious that further confirmation is desirable and experiments are in progress.

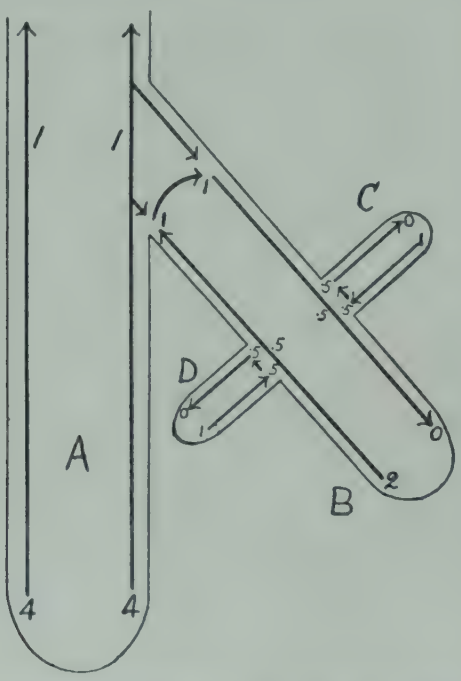


FIG. 5. Diagram to show secondary and tertiary roots.

THEORETICAL CONCLUSIONS.

After these experiments there seems to be nothing unreasonable in considering that the stem is of an "alkaline" nature with electronegative particles in the disperse phase of the plasma membrane and that the root is of an "acid" nature with electropositive particles.

EXPLANATION OF ORIENTATION OF SECONDARY AND TERTIARY ROOTS AND STEMS.

The previous theories of curvature apply only to main stems and roots. It is known that secondary roots grow at a more or less definite downward angle to the vertical under geotropic stimulation, while tertiary roots grow more or less in all directions. Secondary and tertiary stems grow in much the same way, although the

direction of growth is influenced in these cases by heliotropism, the action of which in the root system is negligible for present purposes. Any sound theory of geotropism should be able to yield an explanation of these phenomena with much the same type of protoplasm in the laterals as in the main axes.

Considering first the secondary root B of the primary root A in Fig. 5. According to previous theorisings and experiments we can suppose that a current flows upwards in the cortex of the primary root A as a result of the creaming and potential differences in the apical meristem, which should be present even in the erect root according to the views expressed above. This current being symmetrically arranged produces no "action" current and no curvature. The PD on account of the resistance will decrease as it passes upwards, see Fig. 5, where the PD is supposed to be reduced from 4 to 1 at the base of the secondary root B.

If the secondary root B were placed horizontally it would develop asymmetric potential differences, an EMF and an action current as outlined for the horizontal primary root. Since the meristem is smaller the current would be smaller but it would still have a greater effect in the lower side and the rootlet B would tend to grow vertically downwards. At the point where it joins the primary root A, however, there is a current flowing in the cortex which would enter the rootlet B both in the upper and the under sides, if the potential differences were suitable. This "leakage" of the normal polarity current from A would tend to flow towards the apex of B; in the under side it would meet an opposing current, while in the upper side it would flow or tend to flow in the same direction as the action current of B. The action current and its effects in the upper side of B would, therefore, be augmented by the normal polarity current from A, while the action current in the under side of B would be more or less reduced by the normal polarity current from A, according to the relative potential differences of the current from A and the current in B at the point where it meets the primary root A.

The general effect of the current from the primary root would thus be to neutralise more or less the asymmetric effects of the action current in B, and *the angle at which the asymmetric effects of the action current in the secondary root are neutralised by the leakage of the normal polarity current from the primary root is the angle which the secondary root will make with the vertical.*

An angle which was greater than the angle of balance would increase the strength of the action current and the rootlet would grow downwards. An angle which was less than the angle of balance would result in reversed asymmetric effects from the action of the normal polarity current from the main root and the rootlet would grow upwards.

This stable angle is known to be very much the same when the root system is inverted. Under these conditions the primary root would also be inverted vertically and the current would be similar in strength but different in direction of flow in the primary root; it would still tend to flow into the secondary root. The action current in the secondary root would also be reversed in its relation to the morphologically upper and under sides so that the balance would again be reached when the secondary root had attained the same angle with the vertical as before and, therefore, had the same strength of action current.

It is not necessary to labour this point. Many experiments and observational details in connection with secondary roots are clearly to be explained along these lines, always keeping in mind the point that if the primary root is at an angle to the vertical there will be an *action current* in it, instead of a *normal polarity current*, which may so augment the effects of the action current in the secondary root that it (the rootlet) will curve away from instead of towards the vertical until it has developed an action current sufficiently strong to balance once more the current "leaking" from the primary root.

Considering next the tertiary roots C and D of the secondary root B, the electrical conditions are becoming rather complex. These tertiary roots arise on all sides of an organ which is no longer symmetrical physiologically about its own axis, as in the case of the primary root. Although the total effect in the upper and under sides may be the same with B at its angle of balance, the asymmetric PD is still there. The lateral sides of the secondary root would be in similar electrical condition, but that condition would not be the the same as upper and under sides. There would be a great variety of current strengths in the secondary root which would require to be balanced by the action currents of the tertiary roots before these could reach a stable angle. Taking C and D as examples of such tertiary roots, D would reach its angle of balance when the unilateral effects of its action current (PD 1 in Fig. 5) were neutralised by the inflowing current (PD ·5 in Fig. 5) from B; and C would behave in a similar fashion although in that case the angle of balance would be unstable.

Since the action currents at the angles given in the diagram (Fig. 5) would be somewhat similar in strength (cp. Newcombe, 14, for primary roots), and their effects would be neutralised by the same current strength (PD ·5 in Fig. 5) from both upper and under surfaces; these angles would be the angles of balance and C would grow upwards and D downwards. If C had a downward angle the same as that of D it should theoretically grow downwards but it arises on the upper side and is thus directed upwards before it has developed the motor region which is necessary for geotropic curvature.

Secondary and tertiary stems can be treated theoretically in the same way, always keeping in mind the point that the action current in the lateral branches and the normal polarity current in the main stem are to be considered as reversed in their direction and arrangement as compared with those in the root, so that the secondary laterals take up an upward angle of balance. The action of heliotropic stimulation interferes chiefly with the angles of the tertiary branches, because in these the geotropic action currents are weak compared to those of the main stem and secondary branches.

The action of heliotropic stimulation becomes altogether predominant in the leaf, which may be regarded as neutral or non-polarised as far as gravity is concerned. Buds, flowers and fruits show gravity responses (13, etc.), but the responding region is usually the stalk which can be regarded as a secondary or tertiary stem structure. Food supplies also may interfere in such cases by altering the osmotic pressure, apart from permeability changes, as has been suggested previously (20, pp. 197, 295).

Although this theory of geotropic stimulation and curvature in stem and root thus explains the chief points in the orientation of stems and roots in normal and in experimental conditions, and the orientation of their secondary and tertiary laterals, and although it is also in complete accord with the known facts of the physico-chemical phenomena of protoplasm and cellular tissues, it is recognised that a large field for experimental work is opened up in the verification of details and in the development of the new measure of control over the plant organism which is suggested.

As a theory the suggested differentiation in hydrogen ion concentration of root and stem has very wide applications to cytolysis, acid-tolerant and calcifuge species, immunity from and liability to attack by bacteria and fungi, the development of

intumescences, the effects of acids, alkalies and salts on plants and animals in general and on the permeability of protoplasm in particular and possibly also to epharmonic variation. It provides an explanation, not only for the normal polarity of growth in plants, but also for the changes in geotropic response and in colour which occur in flower buds and other organs. The adsorption of ions by the Brownian particles, which is postulated, furnishes an explanation of the stimulus/response ratio of the Weber Law as modified (24-25) by Waller.

EXPLANATION OF PLATE I.

Fig. 1. Three beans with secondary roots showing negative geotropism.

Fig. 2. Main roots of the bean showing the same.

Fig. 3. Main roots of the maize showing the same.

Fig. 4. Adventitious roots of the maize ; two show slight upward curves.

Fig. 5. The same, five days later, with more pronounced upward curves.

Fig. 6. Maize stems with unbroken coleoptiles showing positive geotropism.

Fig. 7. Controls in a neutral atmosphere : the top specimen has recovered after growing down as in Fig. 6. (specimen on the right).

Fig. 8. Maize stems, showing cytolysis and fungal infection after downward curving had taken place.

Fig. 9. Maize stems showing positive geotropism, the lower specimen did not react at all, either positively or negatively.

Fig. 10. Three of four stems showing the same.

Fig. 11. Four stems all positively geotropic.

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MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER II.—*Continued.*

Foundations of the Mutation Concept.

FROM the standpoint of the mutation concept, *Œnothera lata*, while a critical case in demonstrating the occurrence of germinal changes, differs in several respects from the most frequent and widespread type of mutation, *i.e.*, the type which results in a new Mendelian character. The latter type of change will be considered in greater detail in connection with the origin of dominant and recessive Mendelian characters, mass mutations and parallel mutations. The type of mutation involving an extra chromosome differs from this in the following points. (1) There are present three representatives of the extra chromosomes instead of a pair. A Mendelian mutation, on the other hand, will first appear usually as a heterozygous individual if the new character is dominant, or as an individual homozygous for the new character if it is recessive: that is, a pair of chromosomes only will be involved, one or both of which carry the new factor. (2) As we shall see later, the presence of the extra chromosome determines, at least in large measure, the hereditary behaviour of the form possessing it. (3) Chromosome duplication, viewed as a germinal change, arises through, or at least in connection with, a rearrangement of the chromatic material, resulting from an irregular distribution or non-disjunction of a pair of chromosomes in the heterotype mitosis, while when a Mendelian character arises one must assume it is by an alteration in one element of a chromosome.

Thus while the bearing of the extra chromosome in *Œnothera lata* upon the mutation concept is clear in that, as we have already pointed out, there is a constant relation between the *lata* characters and the additional chromosome, yet the relation of this type to the numerous other forms now known to have 15 chromosomes is by no means so clear, and raises a number of intricate problems. These forms and the problems connected with them will be discussed later. For the moment we are concerned in pointing out some of the other bases of present concepts regarding mutations.

The *gigas* and *semigigas* series of forms, having respectively 28 and 21 chromosomes, again clearly justify the concept of a mutation as a cell change involving a new nuclear structure perpetuated by mitosis. This type of change is now known,

through parallel mutations, in several species of *Œnothera*: but tetraploidy exists in a wide range of wild species, and a doubling of the chromosome series is also known to occur under various experimental conditions which will be referred to later. The forms, such as *lata* and *semigigas*, with an unbalanced chromosome number, will seldom if ever breed true, and such forms can only occupy a somewhat temporary and aberrant place in evolutionary descent. But tetraploidy is a condition of evolutionary significance, as the cytological study of many genera and families already shows. It gave the first hints towards the construction of a phylogeny of the chromosomes, and ultimately it is quite certain that such a phylogeny must be constructed.

While the 15-chromosome mutants produce two types of gametes, and hence are at least dimorphic in their offspring when crossed back with the parent type, the tetraploid forms are also peculiar in their inheritance, giving triploid intermediate hybrids when crossed back with the parent (diploid) type. Such forms are for the most part unstable, and although they occur in nature (*e.g.* the well known natural hybrid between *Drosera rotundifolia* and *D. longifolia*) yet their instability and partial sterility prevent their giving rise to permanent intermediate links between the original diploid species and its tetraploid derivative. Meiotic irregularities in these hybrids may lead to the production of a series of plants with new chromosome numbers, as is well known in the Œnotheras. But seldom will a stable form arise having a balanced chromosome equipment. With the exception of tetraploidy, therefore, none of the types of visible chromosome change so far demonstrated in the Oenotheras are likely to have played a very large rôle in any phylogeny. They are chiefly valuable as a means of furnishing a visible demonstration of the occurrence of germinal nuclear changes.

All the evidence indicates that the great mass of mutations originate as new Mendelian characters. Among such changes in the Œnotheras are *Œ. rubricalyx*, a dominant, and *Œ. gigas nanella*, which in crosses with its parent form *gigas* behaves as a Mendelian recessive. We may consider these two forms as types of Mendelian mutants. On the basis of their inheritance as such, we must assume that they originate through an alteration in a particular locus of one chromosome, a view set forth elsewhere[1] and now generally accepted. The history of *Œ. rubricalyx* has been given in the work cited,[2] but the salient points may be referred to here.

[1] The Mutation Factor, p. 300.

[2] The Mutation Factor, p. 102.

One plant in a large culture of *Œ. rubrinervis*[1] appeared with an extreme increase in anthocyanin pigment, this red being especially conspicuous on the sepals, flower stalk, stem, and the under surface of the leaves, although histological examination shows it to be present in increased quantity in all parts of the plant. The original individual was heterozygous, originating therefore through the union of a mutated with a non-mutated germ cell. The premutation must then be considered to consist in a change, probably chemical, in a locus of one chromosome, and this change probably occurred during some stage of meiosis. Farther than this the matter cannot be analysed at present. The altered chromosome, present in the nucleus of every cell through mitosis, increases the capacity of every cell for producing anthocyanin, as is shown for instance by comparing cells of the chalaza in the two forms.

Through an unfortunate accident, only a few offspring of the original *novum* survived. They were 9 *rubricalyx*, 1 *rubrinervis*, and 2 rosettes classed as "doubtful." The next generation gave three families, with ratios 10 : 5, 14 : 6 and 33 : 11 respectively, all clearly representing 3 : 1 families. This leaves no reasonable doubt that the original *rubricalyx* mutant was heterozygous for one factor for red. For by no possibility can any of the three ratios 10 : 5, 14 : 6 or 33 : 11 be considered to represent a 15 : 1 ratio, while their total, 57 : 22, is clearly close to the 3 : 1 expectation. Also the ratio in the previous generation (which may be taken as probably 11 : 1), from which these three families were derived by selfing certain individuals, while it might by itself conceivably represent a 15 : 1 family, cannot do so really. Because the chances are remote that, if the parent mutant were heterozygous for two factors for red, three of its offspring taken at random as mother-plants of the next generation should all happen to be heterozygous for a single factor (therefore giving 3 : 1 ratios) and none of them homozygous or heterozygous for two factors.[2] The evidence taken as a whole is therefore clear that *rubricalyx* originated in one individual which was heterozygous for a single factor for red.

[1] It now appears (Lutz 1917b) that the form which other investigators, at least MacDougal, Miss Lutz and myself, regarded as *rubrinervis*, differs from the Amsterdam *rubrinervis*, which is a less robust form. Further study by de Vries has revealed several types closely related to *rubrinervis*, which will be referred to later.

[2] If the original mutant were heterozygous for two factors for red, it would give in its offspring 1 plant which bred true to red, to 8 yielding *rubricalyx* and *rubrinervis* in the ratio 15R : 1r, to 6 yielding ratios 3R : 1r, to 1 pure *rubrinervis*. It gave in fact three families all of which were 3 : 1.

Duplicate Factor Mutations.

This fact is thus emphasized because later generations produced some families with 15 : 1 ratios, hence representing two factors for red, in addition to families with 3 : 1.[1] Furthermore, certain 15 : 1 families came from members of families showing a 3 : 1 ratio.[2] These must therefore have been due to secondary mutations. The evidence, part of which has been considered elsewhere,[3] shows with a high degree of probability that, as we have seen, the original mutant was heterozygous for a single factor for red. Shull (1914a), unfortunately, from a study of hybrids between *rubricalyx* and *Œ. grandiflora* which he mistook for pure *rubricalyx*, drew erroneous conclusions regarding the origin and behaviour of this striking form. Another important feature in its history, already mentioned, is the fact that members of a family of *rubricalyx* which contains a single factor for red, as shown by the 3 : 1 ratio, can give rise to individuals which are heterozygous for two factors for red. How this may come about has been discussed under the name duplicate mutation[4].

That two or even three factors for the same character may exist in a given strain, was first shown by Nilsson-Ehle (1909) for wheat, and has since been demonstrated in a number of other forms. Nilsson-Ehle showed for example that while Extra Squarehead wheat has only one factor for red kernels, Sammet and Grenadier have three, and in a later paper (1911) that Swedish Binkel has two. A list of such duplicate determiners has been given by Shull (1914b). It includes glume colour, hairiness of glumes, length of glumes, width of leaves, etc., in oats, and various characters in beet, turnip, gourd, flax, tobacco, bean, pea, velvet bean, wheat, and maize among plants ; also body weight in ducks, fecundity in fowls, skin colour in man, ear length and body size in rabbits, piebald coat colour in mice and the hooded pattern in rats. Of course some of these cases are much better substantiated than others, and the number of cases has since been considerably increased. The Howards (1912) have demonstrated one of the clearest cases of duplicate factors for red in wheat.

Nilsson-Ehle did not consider the origin of this condition of duplicate factors in wheat, but it appears probable that it has the

[1] Gates 1915b.

[2] Some 5 : 1 ratios were also obtained, which are probably to be explained by linkage.

[3] Gates 1915e.

[4] Gates 1915b.

same explanation as the duplicate condition of the factor for red in *Œ. rubricalyx*. There are, as previously pointed out[1], at least two ways in which such a result is likely to have come about. (1) Through a locus in a second chromosome having independently undergone the same change or mutation. (2) An individual which would normally be homozygous for one factor for red (RR′) might, by a mismating of the chromosome pairs in fertilization or after, become heterozygous for two factors for red (RrR′r′). In this way an individual giving a 15 : 1 family of offspring could arise from a homozygous member of a 3 : 1 family. It is necessary to assume that such a regrouping of chromosomes took place at fertilization or soon after, so that the nuclei of the whole germ track[2] would have the same chromosome grouping. The difficulty with this view, and it appears now to be a fatal one, is that it seems necessary to assume that the other chromosomes with which these two "red" chromosomes are mated will differ from them in other factors as well and will therefore introduce new differences in the offspring. Morgan has shown in *Drosophila* that eye-colours so closely alike as to be indistinguishable except by the expert, may arise in different chromosomes, as independent mutations.[3] Hence it appears more probable that these factors for red in *Œ. rubricalyx*, which are as yet quite indistinguishable, may have arisen in the same way through successive parallel mutations in different chromosomes of the same race.

Shull (1914b), however, uses the second hypothesis, mismating of chromosomes, to account for the origin simultaneously of the duplicate condition for triangular capsule form in *Capsella bursa-pastoris* and the mutant *C. Heegeri* with round capsules. If, in the reduction division, the pair of chromosomes containing each a determiner for triangular capsule pass into the same daughter nucleus, this would produce an individual with duplicate factors for capsule form, while the other germ cell, lacking both these determiners, would later give rise to the mutant *Heegeri*. His modified suggestion that both these conditions, (1) duplicate factors for triangular capsule, (2) the origin of a mutant lacking both these

[1] Gates 1915b.

[2] The term germ track, the English equivalent of the German *Keimbahn*, is used to represent the line of cells or cell divisions following each other from the fertilised egg to the pollen mother cells or the eggs. As de Vries pointed out *(Intracellular Pangenesis)*, we may thus think of a pedigree of cells derived chiefly from apical cells and forming a connected system.

[3] In the same way, the factor for red midribs described by Heribert Nilsson (1912) in a derivative of the Swedish race of *Œ. lamarckiana* appears to be different from that in the Amsterdam race.

factors and hence round, could come about through the detachment of the determiner for triangular capsule from the end of one chromosome and its attachment to the end of the next, seems more likely and more in accord with our present knowledge. The difficulty with it as a general explanation is that one cannot suppose that all duplicated factors have been conveniently located on the end of a chromosome, especially where a number have been described for the same organism, as is the case with wheat, maize and tobacco. The most likely hypothesis of the origin of most duplicate factors is then the independent origin of each through a chemical alteration of a locus in a different chromosome.

However, the recent breeding experiments with *Drosophila* have disclosed cases (Bridges 1917) of duplication in which the genetic behaviour is as though a group of genes from the middle of one X-chromosome has become attached to the end of the other X-chromosome in a female. Another exceptional case, discovered by Bridges and reported by Morgan (1919), is explained on the assumption that a piece from the second chromosome has become attached to the middle of the third chromosome. In the resulting race, when these chromosomes separate and recombine in reduction and fertilization, zygotes which receive the deficient second chromosome fail to develop unless they also receive the third chromosome with the additional (duplicate) piece. We are therefore at liberty to suppose that a redistribution of certain chromatin elements, rather than a fresh transformation of a new determiner has taken place in certain instances. But such cases will usually involve a group of factors simultaneously rather than a single one.

Recessive Mendelian Factor Mutations.

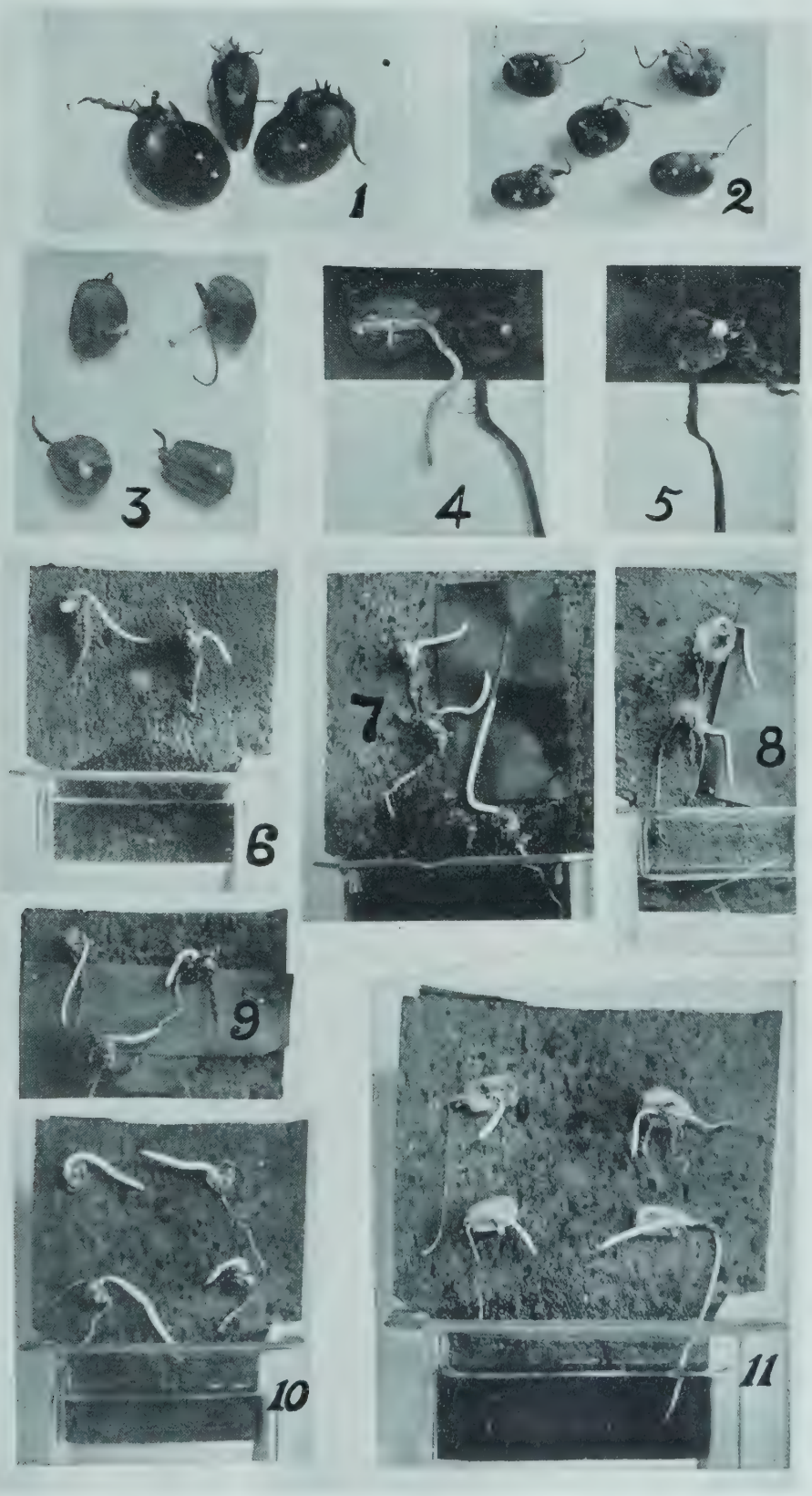
If we turn now to *Œnothera gigas nanella* as the type of a recessive Mendelian factor mutation, the manner of its origin seems clear from its hereditary behaviour. De Vries (1915) has brought together the evidence concerning its behaviour. *Œ. gigas* produces this dwarf in 1—2% of its offspring, *i.e.*, as mutations. But certain individuals of *gigas* are known, from observations of Schouten, Gates and de Vries, to produce as many as 18% of dwarfs. Such individuals are evidently heterozygous, arising from the union of a normal *gigas* germ cell with one which has mutated so as to carry the dwarf factor instead of that for tallness. Theoretically they should give 25% of dwarf offspring but the number is reduced by their lesser viability. This phenomenon of producing in the

offspring a large number of a new form has been called by Bartlett (1915) mass mutation. In such a case it is obvious that the original change or pre-mutation, an invisible change in a germ cell, must have occurred in a plant at least two generations earlier than that in which the mass mutation exhibits itself. The 1 or 2 per cent of mutants arising from other *gigas* plants are the result of the chance meeting of two germ cells both of which have mutated so as to carry the dwarf instead of the tall condition. This interpretation is clearly substantiated by the fact that *Œ. gigas nanella* when crossed with *Œ. gigas* behaves as a simple Mendelian recessive. It has 28 chromosomes, like the parent form.

Thus it would appear that many recessive Mendelian characters originate either as single individuals from the union of two mutated germ cells, or with a frequency approaching 25% in the offspring of individuals which have in turn arisen as a heterozygous combination of a mutated and a non-mutated germ cell.

In races or species where self-fertilization is the rule, a viable recessive mutation is very likely to "come out" in two or three generations, but in many animals, including man, where a large amount of inter-crossing of strains takes place, recessive mutations may accumulate over a considerable period, and some of them may then come out as soon as in-breeding begins. Thus in the case of cross-breeding organisms, it is impossible to say, when a recessive Mendelian mutation appears, how long it may have been carried in the germ plasm in a heterozygous condition without getting a chance to express itself. The premutation may have taken place many generations earlier.

As one more case of a presumptive Mendelian mutation in *Œnothera* we may consider *Œ. brevistylis*. Although it has never actually occurred as a mutation in controlled cultures, yet the fact that it was found by de Vries growing wild with *Œ. lamarckiana* although it ripens practically no seeds, indicates that it must have been derived from *lamarckiana*, with which its pollen crosses freely. In this way it maintained itself for seventeen years. When seeds can be obtained it is shown to breed true, and the chromosomes number 14. De Vries (1913) found it to behave as a simple Mendelian recessive, and Davis (1918) confirms this from a more extensive series of crosses. He finds that the reciprocal crosses with *lamarckiana* are uniform and indistinguishable, the characters of *lamarckiana* being strongly dominant. But measurements show that in heterozygous individuals *brevistylis* has an influence in



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shortening the styles, slightly broadening the leaves and bracts, making the bud cones a little thicker and the sepal tips somewhat shorter. The resulting segregation in F_2 is sharp and complete, but the percentage of *brevistylis* is usually below expectation in all crosses, owing to *brevistylis* zygotes being apparently less viable.

This is a very good example of a type which was able to survive for an indefinite period in competition with its parent form, because while producing practically no viable seeds it was perpetuated by occasional crosses of its pollen giving rise to heterozygous *lamarckiana* plants.

Mutations Arising at or After Fertilization.

De Vries assumes that all mutations take place in the formation of the germ cells, that is presumably at the time of the meiotic divisions, and there is a great deal of evidence that many germinal changes arise at this time. During this period the pairs of chromosomes are being redistributed, and the intricate manœuvres of the chromatin material just previous to this separation of the chromosomes gives an opportunity for a variety of rearrangements and aberrant distributions of particular chromatin particles. That the hereditary behaviour known as *crossing-over*, by which part of the factors which were in the same chromosome cross over to its mate, has its basis in changes occurring at this time has been shown experimentally for *Drosophila* by Plough (1917). He found that by subjecting the females to high or low temperature the amount of crossing-over was increased. Further experiment showed that the critical period, during which crossing-over in the offspring was affected, was during the period of conjugation of the chromosomes in the maturation of the eggs. From this it follows that crossing-over takes place at that time and not earlier.

In the Œnotheras it has been shown that many of the irregularities leading to new chromosome numbers arise during meiosis. The origin of mutations with an extra chromosome and the phenomena of non-disjunction in *Drosophila*, of the sex-chromosomes (failure to separate in meiosis), are cases in point ; also the origin of the supernumerary chromosomes in *Metapodius* (Wilson 1909), which arise through irregularities in chromosome distribution during spermatogenesis. In addition, there is evidence both in plants and animals that germ cells with a double number of chromosomes are occasionally produced, through an alteration in the meiotic phenomena. These matters will be discussed in connection with triploidy and tetraploidy. It will be found that the

hypothesis of de Vries (1913) that triploid and tetraploid mutants arise *only* through the union of germ cells one or both of which is diploid is unnecessary, since both these conditions may arise in other ways.

The period of fertilization is an equally critical time in the life cycle of an organism, and the evidence indicates that a number of germinal readjustments or mutations date from this period. Both triploidy and tetraploidy may perhaps arise at this time or shortly after. It has already been pointed out[1] that in crosses such as *Œ. nanella lamarckiana* and its reciprocal, where both parent types split out in the F_1 generation and both subsequently breed true, it is reasonable to conclude that some determining reaction occurs in the fertilized egg, in which one parental germ cell or the other gains the ascendancy. This was formerly explained by De Vries on the basis of pangens in different conditions. But since the important work of Muller (1918) on balanced lethal factors in *Drosophila*, it is evident that linkage to such lethal factors may explain this result, though more will need to be known concerning such lethal factors in *Œnothera* before the explanation can be applied in detail. Differential sterility depending on whether the lethal factor is linked to (*i.e.*, is in the same chromosome with) the factor for dwarfness or that for tallness, would seem to meet the case.

Concerning the origin of *Œ. lamarckiana* mut. *nanella*, we may assume that it appears through the breaking of the linkage between the dwarfing factor and a lethal factor, for if it were a simple Mendelian recessive we should find occasionally a *Lamarckiana* plant which was heterozygous for dwarfness and gave 25% dwarf offspring. But such are never found in *lamarckiana* although, as we have already pointed out, they do occur in *Œ. gigas*. This suggests that *gigas* has lost some of the lethal factors present in *Lamarckiana*. As a mutant, *nanella* has a frequency of only 1—2%, so that the cross-over between the dwarf and lethal factors must be an infrequent one. The discussion of lethal factors will be taken up again later.

That mutations in other forms may date their origin from fertilization has also been held, and Punnett (1919) has recently concluded that this is the time of origin of the well-known cretin mutation in the sweet pea. This mutation differs prominently from the type in having a straight stigma protruding through a cleft

[1] The Mutation Factor, p. 222.

keel, and it is invariably sterile on the female side. It behaves in crosses with the parent as a simple Mendelian recessive, a total of 80 families in six years giving 4198 normals : 1322 cretins, which is not far removed from a 3 : 1 ratio, the viability of the cretin being evidently somewhat less than that of the normal form.

The cretin appeared in a cross between two white sweet peas, Blanche Burpee with long pollen and Emily Henderson with round pollen. From three purple F_1 plants large F_2 families were raised in 1905. From one of these F_2 families containing 187 plants, the seed of 29 individuals was saved for the F_3 generation. These 29 families in 1906 resulted in 2083 plants, all normal. Seeds for the F_4 generation were saved from 14 individuals of one of the F_3 families numbering 181 plants. The F_4 from these 14 plants gave 1118 plants, one of which was the cretin. This appeared in a family of 52 plants raised from the F_3 plant $304^6/1906$. Thirteen sister plants yielded no cretin in a progeny of over 1000, nor did one appear among the 2083 plants of the F_3 generation. The F_5 of 195 plants grown in 1912 from 9 F_4 plants, also failed to produce one, so it remains an isolated case.

Punnett points out that under these circumstances it is unlikely that the cretin originated from two germ cells, each of which had lost the normal factor, for in that case the parent plant would have been heterozygous, giving 25% cretins, and they would also have appeared in the F_5 or in collateral families. Hence he concludes, in agreement with the argument above, that the cretin plant must have arisen through "some radical alteration in the zygote after union between two normal gametes had already taken place," and that it was "due to a change in the individual at some stage *after* fertilization whereby the factor for the normal flower was either dropped out or altered during the somatic divisions." Since the germ cells of this plant were uniform, it is reasonable to suppose that the change took place in the fertilized egg itself.

Morgan (1919), in discussing this case, suggests that the mutation occurred in one chromosome far enough back in the germ track of the parent individual to give rise to pollen and ovules (say in one flower) each carrying the mutated genes. But in that case other germ cells would have been carrying these genes, and these would surely have appeared later either in the heterozygous or homozygous condition.

As regards *Drosophila*, the great number of mutants it has produced apparently all belong to one type, and behave in the same

way. They are nearly all classed as Mendelian dominants or recessives in inheritance, though in a few dominance is variable and subject to environmental influence. Morgan (1919), states that only 12 are dominant out of over 150. These dominants have each appeared in a single individual. Mutants from recessive genes, on the other hand, usually came to light in about 25% of the offspring of a pair, showing that the pair were both heterozygous for the new factor, which must have arisen at least one generation earlier. Whether both members of a pair of chromosomes undergo the change simultaneously is unknown, since if it occurred in the egg one chromosome will be extruded into the polar body, and if in the spermatocyte the chances are small that more than one sperm from the same spermatocyte will function. Still, as far as it goes, the 12 single mutant individuals suggest that perhaps a single sperm and hence a single chromosome of a pair has the new factor. In the case of *Œnothera lata* and *semilata*, which arise through an irregular heterotype division, evidence is available, for these mutants sometimes occur in pairs, suggesting that the change occurred in a pollen mother cell and that the two resulting 8-chromosome pollen grains both functioned.

Drosophila Mutations.

The evidence for mutations in animals was rather scanty until Morgan took up the study of the fruit fly, *Drosophila melanogaster*, about 1910. The rapid breeding and easy handling of these flies in large numbers, makes it an ideal form for genetic experiments, and combined with this is the advantage that it has only four pairs of chromosomes. It is not, therefore, surprising that in the last decade, Morgan and his pupils have accumulated a mass of breeding data, closely analyzed and correlated, which is unequalled in any other organism. With plants growing only one seed-generation a year, it would probably require 150 years to produce an equal number of generations.

The *Drosophila* work has therefore given us a look into the constitution of the germ plasm such as no annual-breeding plant or animal could furnish in a lifetime. The Mendelian behaviour, sex-linked inheritance, and other features are similiar to those found in many other organisms, so there can be no doubt of the wide applicability of the conceptions of mutations and the germ plasm derived from these experiments. In many respects they are in accord with those derived from the *Œnothera* work. Although the simple Mendelian mutations in the latter are comparatively

few, we have already seen that the behaviour of the others can probably be accounted for on the basis of sterility or lethal factors, explanations which now enter into many features of the Œnotheras. Again, the duplication of a chromosome in *Œ. lata* and other forms is paralleled by the phenomena of non-disjunction in *Drosophila*, although there are certain differences which will be pointed out. But in *Drosophila* the rapidity in breeding large numbers in many generations has made it possible to carry the analysis of the germ plasm much further than in any plant.

In the single species *Drosophila melanogaster*, the "vinegar fly," over 150 mutations have been observed. These include more than 25 factors for eye colour, and many more for body colour and form of wings, while many structural differences are also involved in other mutations. The majority of these have appeared but once. Some mutations are, however, more frequent. White eyes, a mutant from the wild red-eyed fly, are known to have occurred three times in the New York experiments (Morgan, 1919, p. 248) and several times in the cultures of other observers. Vermilion eye-colour has appeared at least six times, "rudimentary" wings five times, cut wing four times, truncate wing frequently but probably owing to different changes. As with the *Œnothera* experiments then, certain mutations repeat themselves, but apparently with much less frequence. This suggests that in *Œnothera* the mutation often appears much later than the germinal change (pre-mutation) which gave rise to it, being suppressed in many cases by lethal factors causing sterility.

A number of cases of probable reversion from the mutant character to the original wild type have occurred, but most of these are uncertain on account of the possibility of contamination. In the experiments of May (1917a) with bar-eye, however, this possibility is excluded. This character is dominant to normal (round) eye, and the reversal takes place with sufficient frequency to eliminate the possibility of error. Reverted individuals give only normal offspring. Bar-eye differs from the normal in having fewer facets, and the stock showed considerable variability. In an experiment in selecting for more or fewer facets, May obtained six full-eyed males and five females heterozygous for full-eye. They were indistinguishable from normal and were explained as simple reverse mutations. In a later paper (May 1917b), however, a more complex explanation of this reversal is favoured. It is assumed that the normal wild fly carries a limiting factor with respect to

facet number, and that by "partial non-disjunction," the factor passes from one chromosome to another (presumably during meiosis) so that one chromosome is without a limiting factor while the other member of the pair has two. The egg retaining the latter chromosome would produce a bar-eyed individual. If in such a race a second non-disjunction occurs, separating the two factors, one chromosome would result having triple factors and one with a single factor. The latter would give a reversion to a full-eyed male or a heterozygous female. But it is doubtful if such a method of explanation by splitting up the factor could be applied to reversions in other factors which show no such variability as bar-eye.

A chemical reversal seems more likely to supply a general explanation of reverse mutations, and this is important in its bearing on the nature of a mutational change. For if a recessive mutant factor can revert to the wild condition, then the mutation was not due to an irrevocable loss of a particle, but rather to the transformation of a particle or locus of a chromosome, first in one direction and afterwards back to the original condition.

As regards the infrequency of simple Mendelian factor mutations in *Œnothera*, it would appear that this is partly due to their presence being masked by the greater number of lethal factors. And since lethal factors must produce non-viable gametes or zygotes, *i.e.*, sterility of pollen, ovules or seeds, this is in accord with the large amount of sterility in *Œnothera*. For this reason, except in the case of mutations involving visible changes in the chromosomes, we can seldom be sure in *Œnothera* that the germinal change in a locus of a chromosome which marks the origin of a mutation, did not happen several or many generations previously. It is this contingency with regard to various mutations that has made it possible to suggest that the phenomena are merely the result of the splitting out of factors acquired in some previous hypothetical cross. This argument has been used, notwithstanding the fact that mutations occur in such well-authenticated and self-pollinated species as *Œ. biennis*.

It is an interesting and significant fact that although *Drosophila*, like most animals, can only be perpetuated by a crossing of two individuals in every generation, while in such species as *Œ. biennis* natural crossing is a very rare event at best, yet the bogey of hybridization which is so often raised as a complete explanation of the mutations in *Œnothera*, has never, so far

as I am aware, been suggested for *Drosophila*. Probably the reason is that in *Drosophila* the evidence is clear that most of the mutations at any rate have had their beginning in the germ plasm at the time they make their external appearance. A great deal of ink would have been spared if it had been recognised that for plants as for animals, for *Œnothera* as for *Drosophila*, mutation is a process *sui generis*, a "spontaneous" disintegration or alteration of elements in the germ plasm which finds certain physical parallels or analogies in the behaviour of the atom of radium and other radio-active substances. To attempt to explain away mutations by assuming that nothing new has really appeared is tantamount to a denial of evolution. Zoologists are fortunate in being free from this bogey, and in being able to recognise that whatever effects crossing may sometimes have on germinal behaviour, mutations take place which have no direct reference to it.

Some of the more intricate details connected with the *Drosophila* experiments will be referred to later. We wish here merely to point out the way in which the plant and animal studies on mutation are reacting on each other for their mutual benefit. The clear-cut conception of lethal factors derived from *Drosophila* has been a great advantage in replacing the more indefinite conceptions of "sterility" in *Œnothera*. Again, the duplication of a chromosome in *Œnothera* is paralleled in several features by the non-disjunction of the sex-chromosomes which sometimes occurs in *Drosophila*.

CHAPTER III.

Forms Having an Extra Chromosome.

For a long time it was generally supposed that *Œ. lata* and forms showing similar characters were the only ones containing an extra chromosome. Fifteen chromosomes had been announced in certain other forms by Miss Lutz (1908), but without convincing evidence. Then a very different form, *Œ. incurvata*, having 15 chromosomes, was described from the Swedish *lamarckiana*,[1] and Miss Lutz (1916, 1917) has more recently published her studies, which seem to show that the occurrence of mutations with an extra chromosome is much more frequent than was formerly supposed. Hance has also (1918) found 15 chromosomes in the mutant *scintillans*. This raises problems with regard to the relationship between these forms.

It was natural to suggest that there might be seven distinct types in this series,[2] with a different chromosome of the haploid series figuring in each case. The number of types apparently with 15 chromosomes is now considerably in excess of seven, but as will be observed from Table I, some of these appear to arise only from *lata* × *lamarkiana*. This is undoubtedly a significant fact.

Now if we call the haploid series of chromosomes in *Œnothera* ABCDEFG and assume that A is the extra chromosome in *lata*, then its chromosome formula would be AAABBCCDDEEFFGG; and when the odd chromosome passes undivided to one pole in the reduction division without further irregularities, the gametes formed will be ABCDEFG and AABCDEFG. That is, there are three members of the A chromosome, two of which enter one gamete and one the other. It seems clear that such 15-chromosome forms as *semilata* Gates, *exilis*, *exundans* and Miss Lutz's type 5365 are derived through a secondary modification from *lata*. The evidence is strong that *semilata* Gates at any rate arises only from *lata* × *lamarckiana*. It appears very probable, on account of its characters intermediate between those of *lata* and *lamarckiana*. and also from its origin only from *lata*, that the extra chromosome is the same in both.

In order to have a *different* chromosome become the extra one in the sense in which it appears to be in *lata*, by selfing this mutant (See Table 1), we must suppose that a gamete, which is, say,

[1] The Mutation Factor, p. 147.

[2] Gates and Thomas, 1914.

TABLE I.

Mutations in *Œnothera* with an extra chromosome.

Parent Form.	Mutant.	Chromosome number.	Author.
lamarckiana, *biennis*, &c.	*lata*	15	Lutz, Gates, 1912. Gates & Thomas, 1914
lata × *lamarckiana* ...	*semilata*, Gates ...	15	Gates & Thomas, 1914
Swedish *lamarckiana*	*incurvata*	15	Gates, 1915a.
	lata	15	Gates & Thomas, 1914
	semilata	15	,, ,,
rubricalyx × *grandiflora*	*lata*	15	
rubricalyx	*lata* or *semilata* ...	unc't'd.	Gates, 1915a, p. 110.
biennis semigigas × *biennis lamk.* × *biennis nanella*	unnamed ...	15	De Vries, 1915b.
	lata hybrid ...	15	De Vries, 1915b.
lamarckiana	*scintillans* ...	15	Hance, 1918.
lamarckiana	*albida*	15	Lutz, 1908, 1917.
lamarckiana	*bipartita*	15	Lutz, 1917.
lamarckiana	modified *oblonga* (type 5509)	15	,, ,,
lata × *lamarckiana* ... *lamarckiana* ...	*nanella lata* ...	15	,, ,,
lata × *lamarckiana* ... *lamarckiana* ...	*subovata*	15	,, ,,
Nanella	dwarf type 2256	15	,, ,,
lata and *lata* × *lamk.*	type 4499 ...	15	,, ,,
lata selfed	*exilis*	15	,, ,,
	exundans		
	type 5365 ...		
lamarckiana	type 2806 ...	15	,, ,,
lamarckiana	*elliptica*	15 (?)	,, ,,
lata × *lamarckiana* ...	*rubrinervis*, de Vries	14+1	,, ,,
lata × *lamarckiana* ...	*aberrans*	14+1	,, ,,

ABBCDEFG, fertilizes one which is ABCDEFG. Such gametes could arise from an $\frac{AA}{ABB}$ meiotic separation in *lata* in the first case, and an $\frac{AB}{AAB}$ separation in the second case, the ABB and AB groups (disregarding the other chromosomes) then uniting in fertilisation to form a nucleus with 2 A's and an extra B, although derived from a plant in which there were two B's and three A's. The chances of this happening are small, especially when we remember that *lata* produces practically no functional pollen grains, and that these nearly all have 7 chromosomes. Nevertheless it is not impossible.

In *lata* × *lamarckiana* the chances of getting a mutant with a *new* extra chromosome are greater than in *lata* selfed, for we may suppose (1) that a 7-egg, *i.e.*, ABCDEFG, is fertilised by a sperm having two members of some other pair than A, the latter condition having arisen through an irregular separation involving the non-

disjunction of that pair in meiosis, *i.e.*, AB ♀ + ABB ♂, or (2) that an AAB egg (*i.e.*, having 8 chromosomes) is fertilised by a BB sperm resulting from a $\frac{BB}{AA}$ segregation in meiosis in *lamarckiana* or (3) that the segregation in the megaspore AAABB is $\frac{ABB}{AA}$, the ABB megaspore surviving and being fertilized by a sperm AB, *i.e.*, the normal type, to give an AABBB individual.

While it is thus possible for a new extra chromosome to arise in the offspring of *lata* or *lata* × *lamarckiana*, yet the chances are considerably greater that the same one will remain the extra one. The probability of such forms as *exilis* and *exundans* depending on the same extra chromosome as *lata*, depends on their frequency in the offspring of *lata*, which is at present unknown.

Returning now to the *lata*-like forms, de Vries (1909) described a form which he called *semilata*, and this arose three times independently from *lata*. One of them when selfed gave 358 offspring, of which 3 were *nanella*, 4 *lata*, and the remainder *semilata*. There is some reason[1] for believing that this form may perhaps have had 16 chromosomes. On the other hand, the writer described what afterwards proved to be a different form[2] under the name *semilata*. This stands midway between *lata* and *lamarckiana*, has 15 chromosomes and is only known to arise from *lata* × *lamarckiana*. When selfed this *semilata* gives *semilata* (15 chromosomes), *lata* (15 chromosomes) and *lamarckiana* (14 chromosomes).[3] The relation between these two 15-chromosome types is therefore a close one, and the differences between them can hardly be due to the presence of a different extra chromosome. It is conceivable, for example, that *semilata* might arise from a *lata* egg having 7 chromosomes + a *lamarckiana* male cell with 8, derived through a fresh irregular division. But this explanation would appear to apply better to other 15-chromosome *mutants*. *Semilata* appears rather like a somewhat modified *lata*, and the fact that, as shown elsewhere[3] it exhibits a series of stages running on the one hand towards *lamarckiana* and on the other towards *lata*, supports this view. We may therefore suppose it originates from an 8-egg + a 7-sperm.

Another important fact in this connection is that *Œ. scintillans*, another mutant from *Lamarckiana*, in now known (Hance 1918) to

[1] See Gates, 1915a, p. iii, footnote.

[2] l.c., p. 112.

[3] Gates and Thomas, 1914, p. 532.

have 15 chromosomes. De Vries showed (1909, Vol. I, p. 244) that this form also behaves in a peculiar way in inheritance, usually giving rise to an average of about 57% *Lamarckiana*, 32% *scintillans* 9% *oblonga* and 1% *lata*. In one family as much as 69% *scintillans* was obtained. It is significant that several of the original *scintillans* mutants were from *lata* pollinated by *Lamarckiana*. From these results it would appear that *scintillans* originates from the union of two germ cells, one carrying 8 chromosomes and the other (or perhaps the same one) carrying the *oblonga* qualities. On the other hand, it is possible that the *oblonga* type to which it gives rise, has 16 chromosomes, as Miss Lutz (1917) suggests. Also, while *lata* had a mutation frequency in de Vries' cultures of 0·413%, the frequency of *scintillans* was only 0·038%.

As predicted in 1915,[1] the cytological study of *scintillans*, resulting in the determination of an extra chromosome in its nuclei, throws much light on its origin and behaviour. It seems reasonable to interpret *scintillans* as arising from a germ cell with an extra chromosome—one bearing the *oblonga* characters—just as we picture *lata* arising from a germ cell with an extra chromosome and one having the typical *Lamarckiana* characters. This will depend, however, on the chromosome counts in the various *oblonga* types, which are at present uncertain. That the offspring of *scintillans* were always found to include 1% or more *lata*, shows a close relationship between these two types, and indicates, though it does not prove, that the extra chromosome may be the same one in both cases. Another alternative is that any chromosome, if present in duplicate in a germ cell owing to non-disjunction in the reduction division, will give the *lata* features if combined with a *Lamarckiana* germ cell or *scintillans* if combined with an *oblonga* germ cell. This is improbable for many reasons.

In regard to the relation between these forms, *lata*, *semilata*, and *scintillans*, we thus appeared at one time to be left with only two alternatives, either that the extra chromosome is the same in every case, as the breeding data suggest,[2] or that any of the 7 haploid chromosomes when duplicated will give the same morphological result. The latter alternative is highly improbable for general cytological reasons. However, while the frequency of *lata* is certainly greater in the offspring of *scintillans* than of *Lamarckiana*, it is conceivable that its unbalanced condition may lead to more frequent chromosome irregularities.

[1] The Mutation Factor, p. 142.

[2] It seems highly probable that in *lata* and *semilata* at least, the extra chromosome is the same.

The Swedish race of *Œ. lamarckiana* also yielded not only *lata* and *semilata* but also another form, having 15 chromosomes, called *incurvata*.[1] One of the latter when selfed yielded 5 *incurvata* and one like *lamarckiana*. In this case there is more probability that a different chromosome was involved as the extra one, since no *latas* appeared in the offspring of *incurvata*. But there is no certainty owing to the small numbers involved, an unfortunate result of the great amount of sterility in all these forms.

Other forms having 15 chromosomes will be considered in the discussion of parallel mutations, but it may here be pointed out that a race of *Œ. biennis* produces a *lata* mutation which is an exact parallel to the *lata* from *lamarckiana*, and which has 15 chromosomes[2]. In the *biennis* from the Holland sand dunes, known to have been naturalized there since the time of Linnaeus, Stomps (1914) obtained a *semigigas* mutant. When pollinated by de Vries (1915b) with pollen from pure *Œ. biennis* without the flowers being castrated, it produced 19 offspring,—one dwarf, 10 *biennis* with 14 chromosomes and 8 of a new unnamed type having 15 chromosomes. The latter shows no resemblance to *lata*, but from the description it appears to have several characters in common with *incurvata*. It strongly supports the evidence from *incurvata* that independent 15-chromosome types exist. Regarding its origin in 8 individuals from a cross, one must suppose that the reduction divisions in the megaspores of *Œ. biennis semigigas* produced embryo-sacs, about half of which contained eight chromosomes in their nuclei and half seven chromosomes, the remainder having been extruded or lost through irregularities in division. That such extrusion was not a haphazard and irregular phenomenon, however, is indicated by the fact that these 8 individuals all belonged to one type.

Another *lata*-like mutant was obtained by de Vries (1915b, p. 186) from *Œ. lamarckiana* × *Œ. biennis nanella*. It had in addition to the marks of *lata* the characters of the ordinary hybrid type *Œ. lamarckiana* × *biennis*, and confirms the conclusions of the writer[3] regarding the origin of *Œ. lata rubricalyx* and other *lata*-like forms in hybrids.

Finally we may consider the important studies of Miss Lutz (1916, 1917) on forms with an extra chromosome. It is to be hoped that her counts of chromosomes, which appear hitherto to have been made almost entirely from root-tips and other somatic tissues

[1] The Mutation Factor, p. 147.

[2] Gates and Thomas 1914.

[3] Gates, 1914, p. 265.

may be supplemented and confirmed by studies of the germ-cells. For, while her counts are probably correct, yet the phenomena of fragmentation of chromosomes in somatic cells make it highly desirable that they should all be checked by observations on the chromosomes during meiosis. She has determined the chromosome number in 234 plants, including sixteen different mutant types, 11 of which types had 15 chromosomes, three had 16, and two were triploid. That *Œ.* mut. *albida* has 15 chromosomes has been verified by counting the number in thirteen more plants. As will be seen from Table I, she finds an extra chromosome also in a new mutant called *bipartita*, in *subovata*, *elliptica* (?) and "type 2806," all from *lamarckiana*. In addition, a second dwarf type, unlike *nanella lata*, is found, *lata* as well as *lata* × *lamarckiana* give "type 4499" with 15 chromosomes, while *lata* self-pollinated produces *exilis*, *exundans* and "type 5365." None of these latter forms are described, so it is impossible to judge of their claims to separate status, but it seems clear that the three forms appearing in the offspring of *lata* selfed are secondary in origin, *i.e.*, bear some special relation to *lata*. All that can be said about these forms at present is that there appear to be at least seven distinct types which might arise through duplication of different chromosomes, and that in addition a number of these types appear to be more closely related to *lata*. This is certainly the case with *semilata* Gates, and probably to a different degree or in a different way with several others. This may be connected with other differential factors, but it is useless to speculate about the matter until the facts themselves are clearer. Mut. *oblonga* apparently has some forms with 15 chromosomes and some with 14. The same is true of *rubrinervis*. In this case the true *rubrinervis* of de Vries, a rather weak form, has 14 chromosomes plus a small one. The form which other investigators have called *rubrinervis*, derived from seeds of de Vries, is taller and more robust and certainly has 14 chromosomes. It is the form of my cytological studies (Gates 1908), the form from which *rubricalyx* originated (Gates 1911), and may be called *rubrinervis* Gates for identification. It is more like the *subrobusta* of de Vries, which is derived from *rubrinervis* × *lamarckiana*, and may perhaps be identical with that form or with the closely related *erythrina* (de Vries, 1919) to be discussed later.

Miss Lutz concludes that a very large percentage of the mutant offspring of *Œ. lamarckiana* have 15 chromosomes, there being both a larger number of distinct types and a higher percentage of mutant individuals with the extra chromosome. One would feel safer

about this conclusion if control counts of chromosomes had been made in the germ cells.

At least two of these reputed 15-chromosome forms, *rubrinervis* de Vries and *albida*, "breed true." Miss Lutz points out that this can only take place (1) by apogamy, of which there is practically no evidence, or (2) when two gametes having different chromosome numbers only (one odd and one even) unite to produce viable seeds. Moreover, it is possible as regards *rubrinervis* that this individual derived from *lata* × *lamarckiana* and having a small extra chromosome may differ in some respects as yet unobserved from other *rubrinervis* mutants derived from *lamarckiana* direct and possibly not having the extra fragment. More critical study of *albida* may lead to a similar result.

A number of other mutants recently described, such as *cana*, *pallescens*, *lactuca*, and *liquida* from *Œ. lamarckiana* (De Vries 1916b), which split in their offspring and are closely related to each other in several features, may contain an extra chromosome. The same may be true of *Œ. stenomeres* mut. *lasiopetala* (Bartlett 1915c). These forms will be considered later.

One of the most interesting results obtained by Miss Lutz (1916), is the existence of two types with a small extra chromosome—a fragment. In *rubrinervis* (one plant) 125 mitotic figures showed the small chromosome, and in 52 of them all the chromosomes, 14^{+1}, could be counted. The small chromosome is constantly larger than in the new type *aberrans*, of which there were two individuals. In one plant 30 figures and in the other 8 figures all showed 14^{+1} chromosomes.

In a former paper (Gates and Thomas, 1914) it was shown that a variety of irregularities occur in the meiotic divisions in pollen formation of *Œ. lata*, *semilata* and other forms which are more or less sterile in pollen. This included cases of fragmentation or pulling apart of chromosomes, particularly the odd one, on the heterotypic spindle. It might be expected that such fragments would occasionally be included in the daughter nuclei, and if they afterwards persisted they might be perpetuated by the mitotic mechanism. This is apparently what has happened in *rubrinervis* de Vries and *aberrans*, and it is significant that these three individuals all appeared in the offspring of *lata* × *lamarckiana*. The writer does not agree with Hance (1918) that they probably represent merely a temporary fragmentation of certain somatic chromosomes. Obviously if new forms can arise having gained a

small chromosome fragment, others may have lost a fragment; and this renders probable another type of germinal change, in which the redistribution of fragments of chromatin may take place. It was formerly pointed out (Gates and Thomas 1914) that all these "irregularities" will become the basis of germinal changes if they are perpetuated by mitosis. Some of the differences between 15-chromosome types may yet be explained on this basis.

This brings us to another subject closely connected with the extra chromosome, but which concerns also the question of chromosomes constancy in *Œnothera*. Hance (1918), in the paper already referred to, has studied variations in the number of somatic chromosomes in *Œ. scintillans*. The writer[1] first pointed out such variations in the somatic cells of *Œ. lata*, the number ranging from 12 to 20 or 21. Hance finds that the number of separate bodies in metaphase ranges from 15 to 21, the higher numbers being produced by transverse segmentation of certain of the chromosomes. This matter is of minor importance and will be referred to later. A fact of more interest is that more or less constant differences are found between the lengths of the different chromosome pairs in the group of 15. The pairs of chromosomes form a graded series, each somatic pair differing in length from the next longer by about 9%. This conclusion is based on careful measurements of enlarged drawings of the metaphase chromosome group in 114 somatic cells from different individuals, selected on account of their special clearness and flatness. Of these cells 51 or 45% contained 15 chromosomes, and in each case the sum of the lengths of all the chromosomes was approximately the same, showing that increase in number was due to transverse fragmentation. This demonstration of constant differences in the length of the somatic chromosomes is an important advance in our knowledge of *Œnothera* chromosomes. While differences in size have been previously observed, they have been assumed to be due merely to fluctuation, not being great enough to demonstrate except by comparison of measurements from many cells.

Hance assumes that the odd or extra chromosome in *Œ. scintillans* is the shortest of the 15. It might equally well be the longest so far as his data show. His only direct evidence is the difference in total length of the chromosomes in the two telophase groups of 7 and 8 chromosomes respectively in the heterotypic mitosis of the pollen mother cells. This difference is

[1] Gates 1912b.

2·6 units, but since the chromosomes of the germ cells are shorter and stouter than in the somatic cells this difference cannot be directly compared with the length of the odd chromosome. Hance also concludes that there is no evidence of pairing of the somatic chromosomes. In this we cannot agree, as we believe that in other *Œnothera* forms the pairing, though weak, is sufficiently indicated in certain cases so that the extra or unpaired chromosome may sometimes be directly determined by this method (see Gates and Thomas 1914, pl. 35, Figs. 5, 6, 7, 10, 11, 15). Again, we have not found that accurate drawings of the chromosomes will show them to be of uniform width with even margin throughout, as Hance's figures would indicate, although the departure from uniformity in width is not. as a rule, great.

Coming now to the question of chromosome number in somatic tissues, it would seem at first impossible to reconcile the apparently contradictory results of Hance and Miss Lutz. A critical study has been made of the process of chromosome fragmentation in somatic tissues, although only incidental references to this work have been published.[1] We believe Hance has over estimated the significance of these somatic segmentations. We observed numerous "clear areas" and constricted portions of chromosomes, but the segments were almost invariably in alignment, showing clearly which belonged to the same chromosome. Moreover, delicate linin connections are usually visible connecting the two segments. Miss Lutz (1916) has made similar observations. Constrictions or incomplete segmentations have also been studied in *Vicia Faba* by Fraser and Snell (1911) and Sakamura (1915). In nearly all such cases it is clear which portions make up a given chromosome, and so it is much more sound to treat them as a whole chromosome than to attempt to rearrange these "fragments" on a hypothetical basis from measurements. Formerly we observed no segmentation of chromosomes in prophase nuclei, but more recently the writer has observed several cases of fragmentation in prophase. Nevertheless, we are inclined to look upon the phenomenon as a temporary one, related only to the mitotic cycle, and the segmentations in the prophase of one mitosis as probably bearing no relation to those of the next to follow. The name "extra" or "supernumerary" chromosomes applied by Hance to these segments is not a suitable one, for the actual number of whole chromosomes can be determined without difficulty by observation, as Hance himself has done in *Œ. scintillans*

[1] Gates and Thomas 1914.

The determinations of chromosome numbers from root tips by Miss Lutz are therefore probably correct, although it is certainly desirable that they should be confirmed by study of the germ cells. Although Hance regards the diminutive extra chromosomes of Miss Lutz in *Œ. rubrinervis* De Vries and *Œ.* mut. *aberrans* as mere temporary fragments, yet the evidence seems to indicate that they are permanent products of a fragmented meiotic chromosome dividing by mitosis, and therefore present in every nucleus. Their constant difference in size in the two forms also supports this view.

Summing up the results regarding 15-chromosome forms of *Œnothera*, we may conclude that while several of the types have probably arisen from *lamarckiana* through having different chromosomes as the extra one, yet several others, which have appeared only in the offspring of *lata* × *lamarckiana* or of *lata* selfed, evidently have a closer relationship to *lata*, than to any other form, and *semilata* Gates at least probably has the same extra chromosome. The differences between the other forms may be accounted for partly by the presence of other factors or mutant characters in addition to the extra chromosome, and partly by fresh rearrangements of the 15 chromosomes.

The same irregular meiotic division, or non-disjunction of a pair of chromosomes, also takes place no doubt in other forms, and may be expected to lead to the appearance of occasional aberrant members in other species. Winge (1917) apparently found such a case in *Staphylea pinnata*, which has 12 pairs of chromosomes, but one haploid group with 13 was found in pollen formation. Also in *Cornus glabrata*, anaphase groups of 11 and 12 were observed. Nawaschin (1911) found in the meiotic division, in the pollen mother cells of *Tradescantia virginica* that one pair of chromosomes in the heterotype division is left near the equator, where it forms a vacuole which later becomes included in one of the daughter cells. He finds it dividing later, so that two cells of a tetrad usually receive 11 chromosomes and two 11 + this body, which is called a chromatin nucleolus or heterochromosome. But the brief account leaves many points undetermined. In the pollen formation of *Callitriche verna*, Winge (1917) has described somewhat similar conditions. The diploid number of chromosomes is 16, and in the heterotype division 7 pairs are usually distributed regularly, while the other two frequently pass to positions in line with the equatorial plate but far from the spindle, where they form nuclei.

When cell walls are formed later a hexad of pollen grains is frequently produced, four large ones containing seven chromosomes and two small containing one or two chromosomes each. It is doubtful if any of these pollen grains are functional—regular meiosis takes place occasionally—but it is interesting that a pollen grain with only one chromosome, though diminutive, can still form its exine covering in an apparently normal manner. And such irregularities always make it possible that an extra chromosome may find its way into one of the daughter nuclei, as in the origin of *Œ. lata*.

WHAT IS THE SIGNIFICANCE OF THE EFFICIENCY INDEX OF PLANT GROWTH?

By Franklin Kidd, Cyril West and G. E. Briggs.

[With Two Figures in the Text]

In a recent paper under the title of The Compound Interest Law and Plant Growth, V. H. Blackman (1) has suggested that the dry-weight of an annual plant increases at continuous compound interest, expressed mathematically by the formula $W_1 = W_0 e^{rt}$ where W_1 is the dry-weight of the plant at the end of the time t, W_0 the initial seedling or seed weight, the rate of interest and e the base of the natural logarithms.

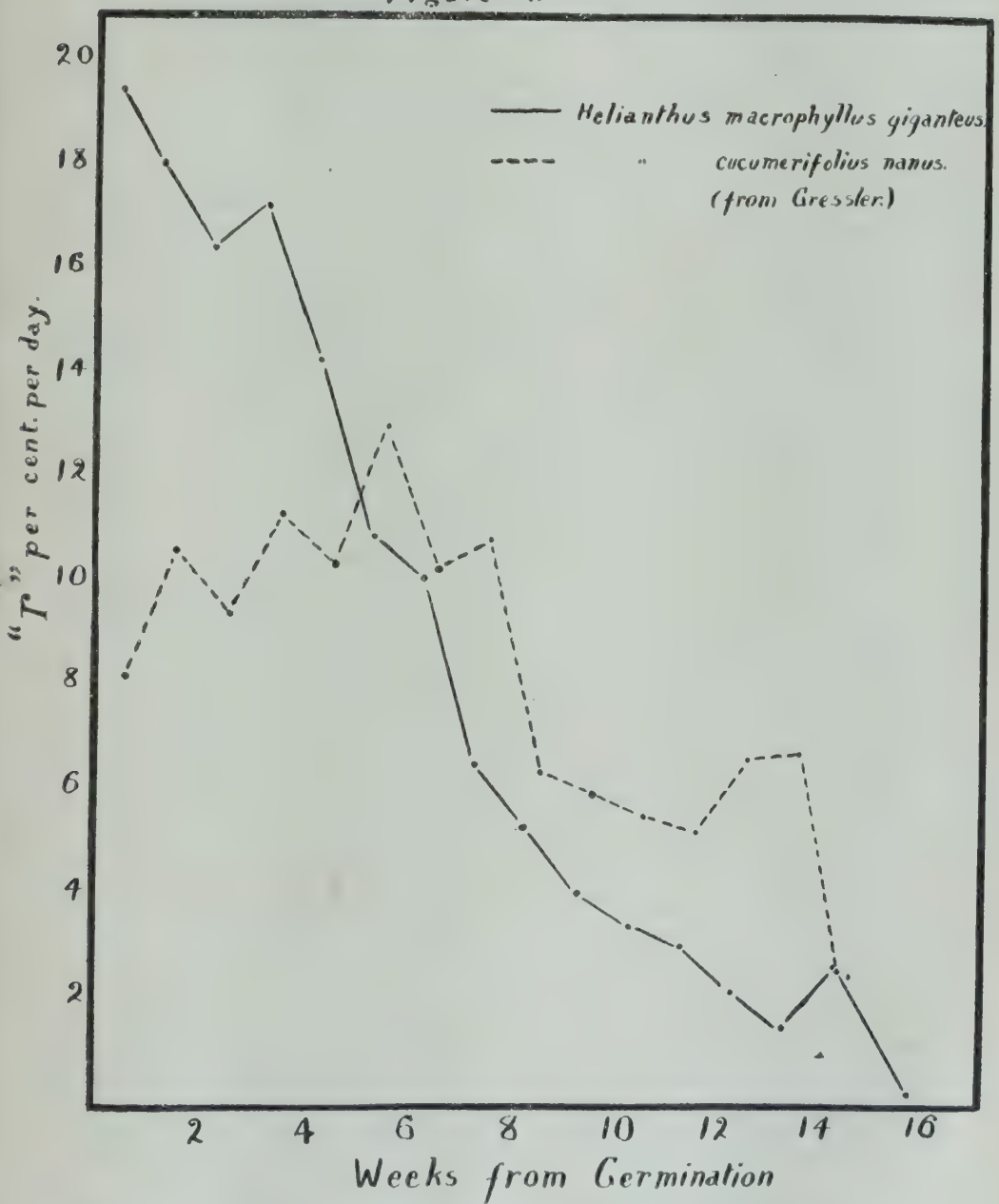
Subsequently a paper by Brenchley (2) has appeared in which the writer has applied this formula. Although the conception of plant growth as a process similar to that of money increasing at compound interest is a useful one, and indeed was put forward by two of the present writers in a previous communication (5), we think it is already clear that a more complete analysis of existing data on plant growth does not warrant so rigid an application of the conception as that made by Blackman and adopted by Brenchley.

The present writers have just carried out a detailed analysis of the carefully recorded growth data of Kreusler and his

co-workers (7) who worked with a large number of plants, and have also analysed in full Gressler's (4) data for *Helianthus*. This is now in the press (3).

In the present note we wish to point out briefly what are the implications of the compound interest formula and to indicate how

Figure 1.

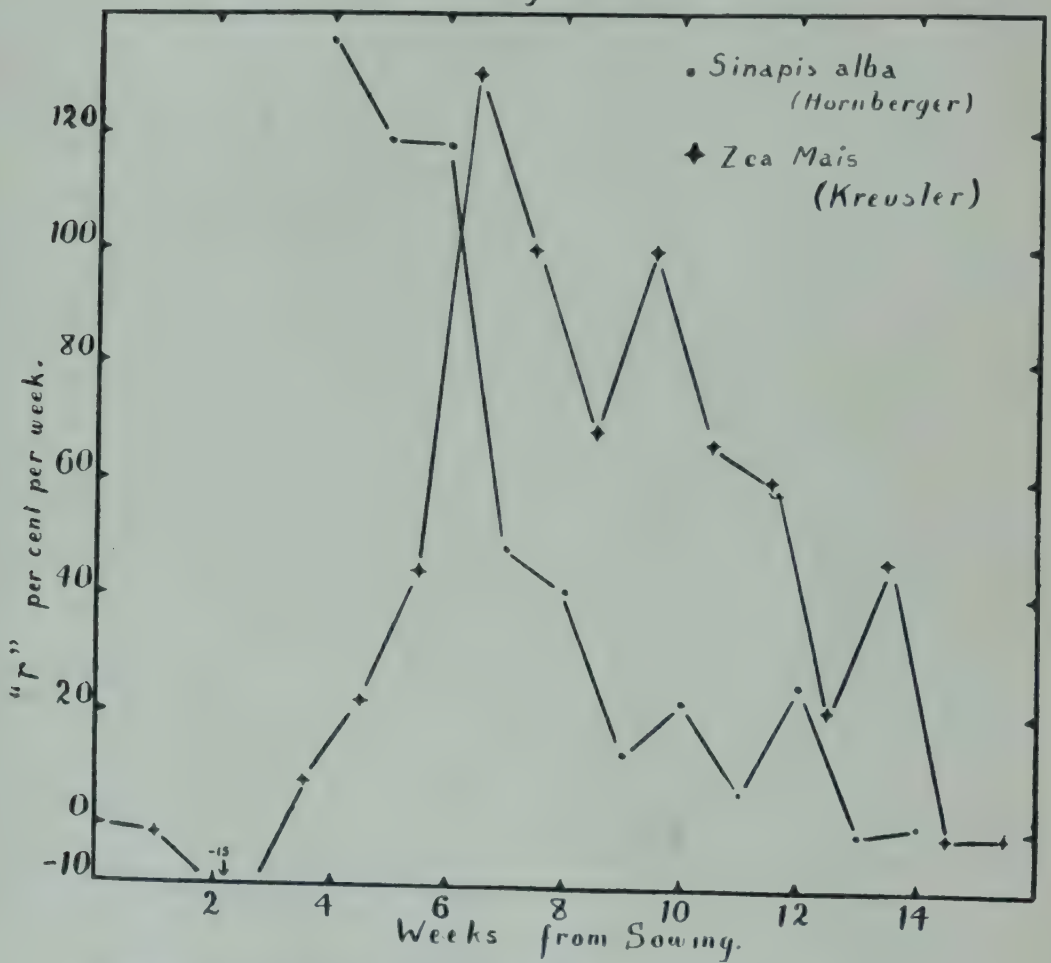


slightly these concord with the behaviour of such plants as have been so far investigated.

In figures 1 and 2 graphs for *Helianthus* (Gressler), *Zea Mais* (Kreusler) and *Sinapis alba* (Hornberger) are presented, the rate of interest from week to week being plotted against time.

If the compound interest law be applicable to the growth of a plant, the rate of interest[1] from week to week, calculated upon the assumption that the plant is working at continuous compound interest, will be constant. If this rate is plotted against time the result it will be a line parallel to the time axis. These graphs show that the rate of interest so far from being constant throughout the life-cycle of the plant, goes through a definite series

Figure 2.



of changes which are correlated with progressive stages in the morphological development[2]. Moreover the indications are that as a general rule the rate does not remain approximately constant even for short portions of the life-cycle of the plant.

[1] The rate of interest is calculated according to the following formula $\frac{\text{Log}_e W_2 - \text{Log}_e W_1}{t} = r$ W_2=Dry weight at the end of the week. W_1=Dry weight at the beginning of the week, t=1 if the rate is weekly, 7 if daily., e is the base of the natural logarithms, and r is the rate of interest.

[2] For a more complete discussion of this question the reader is referred to (3).

It is clear that the growth of a plant obviously does not follow the compound interest law in any exact sense as implied by the equation of Blackman. It is, of course, possible to calculate the rate of interest from week to week as if the plant did follow this law, as has been done in the case of the above figures. The index r then is not a constant but a function of time or of the stage of morphological development.

Blackman says that "The rate of interest (r of the equation) is clearly a very important physiological constant. *It represents the efficiency of the plant as a producer of new material*, and gives a measure of the plant's economy in working. The rate of interest, *r*, may be termed the *efficiency index* of dry weight production. . . . . It may also be termed the 'economy constant' of the plant; it is of course comparable to the velocity constant of a chemical reaction." The impression given by this paragraph and indeed throughout the paper is that the "efficiency index" has a physiological significance and is a constant which provides us with an important standard of comparison between plants of different species and between plants of the same species grown under different conditions.

The value of r can be determined over the whole or any part of the life-cycle. Limitations of experimental method make it impossible to observe results over short enough periods to allow the values of r to be an absolutely correct representation of actual rates, but the shorter the period the more closely do the values of r approximate to these. If a long period is taken the value of r does not represent any actual rate of increase, but merely the rate at which the plant would have had to accumulate dry material if it had increased at a constant rate of continuous compound interest throughout the period.

As indicated by Fig. 1 and as made clear by Table 1 the average value of the efficiency index for any period depends upon the period taken, and moreover in comparing one plant with another the ratio of these averages varies with the period taken. This shows that an average is not a constant for a plant nor is it a standard for comparison with other plants.

We will now consider whether the rate of interest at any point in the life-cycle calculated for the shortest possible time, gives any indication of the efficiency of the plant when comparing it with other plants for which the rate of interest is similarly calculated. The answer is in the negative, for the reason is that any

definite time the rate of interest depends not only upon the species of plant and upon the external conditions but also upon the stage of morphological development reached and upon the previous history of the plant.

The only way in which plants can be compared is by a comparison of the whole series of efficiency indices throughout their life-cycle. From such comparison useful deductions can be drawn, as the present authors have shown (3), and in a broad way the general efficiency of plants can be roughly compared.

From an economic point of view it may be suggested that r would be a useful comparison if calculated over the complete life-cycle, but here the essential idea of the "Substanzquotient" put forward by Noll and his pupils is far preferable, as it simply states the ratio of final weight to seed weight divided by time, and makes no assumption as to the rate at which the addition to dry material has been made. Unless time is of importance the ratio of final weight to seed weight is sufficient.

In order to show definitely the uselessness of r averaged over an arbitrary period or of the "Substanzquotient" for that period as a standard of comparison of the efficiency of different species we have taken the same results as those quoted partially by Blackman and have tabulated them in full (Table 1). The weights of the seedlings on germination, the weights of the plants after approximately equal periods and the efficiency indices calculated for various periods are given. The efficiency index from week to week for *Helianthus macrophyllus giganteus* and for *Helianthus cucumerifolius nanus* have also been calculated and are reproduced graphically in Fig. 1.

Column 4 shows that the average efficiency index for the first four and a half to five weeks is practically the same for four of the species but much smaller for *H. cucumerifolius nanus*; column 8 shows that the same four species after about 8 weeks still agree in having roughly the same efficiency index, and that at the same time *H. cucumerifolius nanus* is less, but whereas *H. cucumerifolius nanus* has maintained, and even slightly increased its r as compared with the first period, the other four species have all fallen off. Column 12 gives the average efficiency index up to the time of the final record of dry-weight. Whether the experiment was terminated at that point because the plants had completed their growth or whether for other reasons cannot be stated with certainty. Since the dates of the final record vary considerably,

TABLE I.

Variety of *Helianthus annuus* used.	Weight of Seedlings at Germination.	Dry-weight after 4½–5 weeks' growth.	'r'	Dry-weight for period selected by Blackman.	'r'	Dry-weight after 7½–8 weeks' growth.	'r'	Dry-weight after 12½–13 weeks' growth.	'r'	Final Dry-Weight	'r'	Final Dry-weight over Dry-weight of Seedling.
Helianthus uniflorus giganteus	0·0325 gm.	(31)* 5·868 gm.	16·8	(38)* 17·33 gm.	16·6	(52)* 46·2 gm.	14·0	(87)* 202·3 gm.	10·0	(115)* 239·1 gm.	7·75	7,357
Helianthus nanus ...	0·0347 gm.	(31) 6·15 gm.	16·7	(38) 14·80 gm.	16·0	(52) 42·2 gm.	13·7	(90) 128·7 gm.	9·1	(90) 128·7 gm.	9·1	3,710
Helianthus cucumerifolius nanus	0·00106 gm.	(34) 0·0361 gm.	10·4	(56) 0·401 gm.	10·6	(56) 0·401 gm.	10·6	(91) 3·38 gm.	8·9	(107) 6·94 gm.	8.25	6,548
Helianthus macrophyllus giganteus	0.0234 gm.	(33) 6·772 gm.	17·2	(33) 6·772 gm.	17·2	(54) 46·9 gm.	14·1	(89) 170·0 gm.	10·0	(116) 235·0 gm.	7·95	10,040
Helianthus arboreus giganteus	0·0190 gm.	(34) 4·850 gm.	16·3	(41) 14·70 gm.	16·2	(55) 45·0 gm.	14·1	(90) 134·0 gm.	9·9	(116) 285·0 gm.	8·3	15,000

* The figures in parenthesis represent the number of days' growth for which the acccompanying dry-weights are given.

the indication seems to be that the reason for terminating the experiment was completion of growth, not weather conditions. An inspection of this column will show that *H. cucumerifolius nanus*, which for all previous periods had a considerably lower average efficiency index, now has one as high as that of *H. arboreus giganteus* and actually larger than that of *H. macrophyllus giganteus* and that of *H. uniflorus giganteus*. Column 6 gives the efficiency index for the periods during which it is at a maximum and approximately constant for each species. It should be noted that the length of this period varies considerably. Finally, the last column gives the ratio of final weight to seedling weight, which after all is the value of most importance economically. A consideration of the variations in the relative values of r will show how misleading it is to state from an inspection of column 6 alone, as Blackman does, that *H. cucumerfolius nanus* has a lower efficiency and that the dwarfness of this plant is due to this lower efficiency as well as to its smaller seed. It certainly has a lower efficiency when compared with the other four species over these periods, but when compared over the whole life-cycle it has a higher economy of working than two of the other species.

Again, it is obviously misleading to compare two plants over different portions of the life-cycle for each. For example, for the period of fifty-six days *H. cucumerifolius nanus* has an average efficiency index of 10·6 whereas *H. nanus* for a period of ninety days has an average efficiency index of 9·1, thus indicating that the former has a greater economy of working: whereas comparisons for any equal period for the two plants or for the complete life-cycle show that *H. nanus* has the greater average economy of working.

Brenchley's Application of the Compound Interest Law.

In Brenchley's work two series of experiments, with mustard and barley respectively, were carried out to find the effect of competition upon plant yield. For this purpose a varying number of plants were grown per pot. The seeds were sown in double quantity and at germination were thinned out to the number per pot required. In the case of mustard (species not given) the plants were harvested after 59 days, in the case of barley after 117 days. In the case of mustard at the time of harvesting "a definite gradation of maturity occurred according to the number of plants in the pot. The single plants (per pot) were very strong, sappy, exceedingly tall and decidedly less mature than any others. . . . . In

most cases only the lowest flowers were fully developed. . . . . The five plants per pot were of medium strength only . . . . . and were the most mature of all. . . . . The flowers were fully out, and many on the main stem had begun to form fruit."

In the case of the barley " the thinly seeded plants were better developed and much less mature than the more crowded specimens."

The author gives the dry-weights of the plants at the time of harvest and the efficiency indices calculated by Blackman's formula, but she does not give the seed weights.[1] As our previous discussion has shown, the average efficiency index for a given plant tends to decrease with increasing maturity, and consequently it is misleading to compare the one plant per pot which was decidedly less mature, with the other plants (other numbers per pot) which were more mature. Possibly, had the whole lot been grown to maturity—the five plants per pot would have taken less time—the average efficiency indices would have been much closer together or might have been the same.

Again, one may be tempted to compare the mustard with the barley. For this purpose the efficiency index is of no use since the plants (mustard and barley) were grown for different periods and had reached different stages of maturity.

The efficiency indices as given by Brenchley, if her seed weights were the same, are simply the logarithmic functions of the final weight divided by time, the time for each set of experiments being the same. It is quite clear that from the point of view of comparing the effect of different seedings per pot in Brenchley's particular experiments the efficiency index has no advantage over the simpler method of giving final dry-weights, assuming the seed-weights were the same, but rather the reverse, because the former implies some physiological significance of the figures given for the efficiency indices.

SUMMARY.

A careful consideration of existing data upon plant growth does not warrant a rigid application throughout the whole life-history of a plant of the compound interest conception of plant growth advocated by V. H. Blackman and formulated in the equation $W_1 = W_0 e^{rt}$. The value r regarded by Blackman as a

[1] We have calculated the seed-weights from the efficiency indices and dry-weights given by Brenchley. Whereas the seed-weights in the case of barley are all exactly the same (55 mgs.), in the case of mustard (variety not stated) the seed-weights form a descending series starting from the one plant per pot (18·3 mgs.) and ending with the five seeds per pot (15·5 mgs.)

physiological constant and as an index of efficiency is not really constant at all in the plants which have been investigated. This index is of no value in comparing the efficiency of different plants, except over strictly comparable times and phases of development, so that the application of the formula by Brenchley in comparing plants of different degrees of maturity is not valid.

Botany School, Cambridge. *February, 1920.*

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THE SIGNIFICANCE OF THE EFFICIENCY INDEX OF PLANT GROWTH.

By V. H. Blackman.

BY the courtesy of the authors, Messrs. Kidd, West and Briggs, I have seen in typescript the paper, which appears in this number of the New Phytologist, entitled "What is the Significance of the Efficiency Index of Plant Growth?"

The main point of the paper on The Compound Interest Law and Plant Growth, which recently appeared in the *Annals of Botany* (XXXIII, 353, 1919) was to stress the view that no conception of the growth of an annual plant was satisfactory which did not take into account the fact that the capacity for dry weight production increased with time on the compound interest principle. Accordingly it was suggested that the best way of comparing the activity in dry weight production of two plants was to compare the rate at which the material already present could produce new material. On the assumption that the material was added continuously—an assumption which is, of course, only an approximation to the truth except in the case of plants grown in continuous light—a formula was put forward by which this activity, or the "efficiency index" as it was termed, could be calculated.

In their paper Kidd, West and Briggs call in question the value of the efficiency index as a measure of a plant's activity on the ground that the index is very variable. That the efficiency index is a variable quantity is, of course, obvious, for it must be markedly affected by external conditions; by light deficiency, for example, it can be reduced to zero or even to a minus quantity. Also Gressler's results, which were quoted, showed clearly that the efficiency index fell off markedly in later periods of growth.

The marked fluctuations in the index which have been demonstrated by Kidd, West and Briggs for Maize, Mustard and Sunflower, and by Brenchley for the Pea (in a paper in the forthcoming number of the *Annals of Applied Biology*, Vol. VI, No. 4), are of great value in that they provide a deeper analysis of the growth-relations of the plant at various stages. These fluctuations in the efficiency of the plant do not, however, affect the value of the efficiency index, for it is obvious, and it is indeed clearly stated in the original paper (pp. 357 and 358), that all that the calculation gives is the *average* efficiency index. Kidd, West and Briggs state that the efficiency index if a long period is taken "does not represent any actual rate of interest, but merely the rate at which the plant would have had to accumulate dry material if it had increased at a

constant rate of continuous compound interest." This is of course perfectly true and state the nature of the index very clearly. The efficiency-index-like averages in general is only an abstraction, but it is none the less valuable as a basis for comparison.

The three authors further insist that the *only* way in which plants can be compared is by a comparison of the whole series of efficiency indices throughout their life-cycle. This is rather a large claim. Surely in the absence of such full data the comparison of the average efficiency for larger periods or for the whole life-cycle is of value. And even if the daily or weekly efficiency indices are available for the whole life-cycle it is still useful for purposes of comparison to sum up the activity of the plant for longer periods by calculating the average efficiency index on the supposition that it is constant throughout those periods.

The efficiency index was described as an "important physiological constant." The word "constant" might have been put in inverted commas in the original paper, for the only real constants of a living organism are, no doubt, those of the physical and chemical processes of metabolism. There is, however, a precedent for the use of the term for the rate of an important physiological process, for Dugger, in his book "Plant Physiology" (p. 255), uses the term for the average rates of such physiological processes as photosynthesis, transpiration, etc. It should have been clear that the use of this term "constant" in relation to the efficiency index did not, and could not, imply that the rate of addition of new material was an invariable quantity.

In supposing that the index would be the more accurately determined the shorter the period of time under consideration, the three authors are pressing too closely the analogy with a physical constant, and exhibit a failure to realise—and this seems to lie at the basis of their criticism—that the index is almost necessarily only an average of a number of widely differing rates.

Data obtained from daily periods would not necessarily be any more valuable than those for longer periods, nor hourly data any more valuable than daily ones. A little consideration will show that, except for plants grown under external conditions which are kept artificially constant, the rate of increase of material must wax and wane with the rising and setting of the sun, and that during the night the rate becomes a negative quantity. The efficiency index when applied to plants growing under natural conditions is thus necessarily only an average or conventional measure of the plant's

activity in the production of new material.[1] It is clear that owing to the marked fluctuation of the index over even such a short period as 24 hours some such convention is essential if we are to compare the activity of different plants.

It has further been suggested in criticism that "the essential idea of the 'Substanzquotient' put forward by Noll and his pupils is far preferable, as it simply states the ratio of final weight to seed weight divided by time, and makes no assumption as to the rate at which the addition to dry material has been made." In relation to this criticism it must be pointed out at once that the last statement cannot be accepted. A formula in which the final weight is divided by seed weight and by time implies that there is a linear relation between time and weight (*i.e.*, that the increase of weight is an arithmetical progression) just as definitely as does the formula I put forward carry the implication that the relation between time and weight is a logarithmic one (*i.e.*, that the increase of weight is of the nature of a geometrical progression). A simple formula is no less based on theory than a more elaborate one.

The question as to which formula is the more suitable is simply the question as to which hypothesis most closely fits the facts. That plants do to a large extent add new material on the compound interest principle can hardly be denied. It would seem also that annual plants when growing under favourable conditions add the main mass of their material at a rate which constantly increases with time (see for example, Fig. 4 of Dr. Brenchley's in the forthcoming paper already cited). A formula which takes this mode of increase into account by assuming an average or conventional index, would seem then more satisfactory as a comparative measure of efficiency than one which implies the addition of new material at a constant rate.[2]

The authors have also criticised the exhibition in the original paper of the data from Gressler's work on *Helianthus*. The times chosen for the various species were those for which it appeared that the geometrical increase of dry weight was most marked. They served to bring out the marked difference in the economic rate at which these plants were working *during these periods*. The

[1] The use of the term "constant" can on this ground be defended as *literally* correct, since for any given experiment and any given period the index is an absolute constant, albeit a hypothetical one.

[2] It may be that to some plants growing under unfavourable conditions, or with a long period of slow growth in the latter part of their development, the simple "arithmetical" formula would more aptly apply. Even in these cases, however, for purposes of comparison with other plants the compound interest formula may conveniently be used.

fluctuations in the efficiency index, on which the three authors rightly lay stress, clearly indicates that caution must be exercised in making deductions as to a plant's *general* economy of working from the efficiency index calculated over short periods, but the efficiency index does nevertheless give a measure of the plant's *average* efficiency *during any particular period.*

As was pointed out in the original paper we know nothing of the experimental errors of Gressler's results and he admits that the number of plants used for the dry weight determinations was sometimes very small so that the results cannot with assurance be subjected to a very close analysis. Up to the $7\frac{1}{2}$-8th week the dwarfness of *H. cucumerifolius nanus* is certainly due to a low efficiency index as well as to a small seed weight, as the table provided by Kidd, West and Briggs shows, for the index of this plant is markedly lower than that of any of the other four forms; and even up to the $12\frac{1}{2}$—13th week the index of this particular species is still the lowest. It is true that when the last determination is made the indices of both *H. uniflorus giganteus* and *H. macrophyllus giganteus* fall below that of *H. cucumerifolius nanus.* It is to be noted, however, that during the last period of growth shown in the table the dwarf form more than doubles in weight, while the two other forms increase only 18% and 38% respectively, in spite of the fact that the period in question is longer. It is obvious that the average efficiency index over the whole period of growth has been reduced, both in the case of *H. uniflorus* and *H. macrophyllus*, by a long period of slow growth in the last stage of development. Whether this period is absent in *H. cucumerifolius nanus* or the plants were cut down too early to exhibit it is not clear; the latter would seem more probable.

The three authors have also criticised Dr. Brenchley's use of the efficiency index in exhibiting some of her results. In the case of the barley plants she investigated the plants differed in maturity in relation to harvesting, but it is clear that they had practically reached their full size, and in Dr. Brenchley's opinion it is probable that in all of them increase of dry weight had ceased. The mustard plants if allowed to continue growth would certainly have increased considerably in dry weight, but as already stated the efficiency indices do give a measure of the economy of working of the various sets under the given conditions and for the given period, and so exhibit the effect of external conditions more accurately than do the final dry weights alone.

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PHYSIOLOGICAL ANATOMY OF XEROPHYTIC SELAGINELLAS.

BY J. C. TH. UPHOF, PH.D.

[WITH TEXT-FIGURES, I-XII.]

THE writer has made an attempt to obtain data on the behaviour of xerophytic Selaginellas, by investigations carried out in the deserts of Southern Arizona, California, Northern Sonora, Mexico, and on bare mountain tracts and rock outcrops in eastern and south-eastern Missouri. The laboratory work was conducted at the University of Arizona, and at the Herbarium and Jodrell Laboratory at the Royal Gardens, Kew. The author is much indebted for kind help to Sir David Prain, Director, and Dr. Arthur W. Hill, Assistant Director of Kew Gardens, to Dr. Otto Stapf, Curator of the Herbarium at Kew, to Mr. L. A. Boodle, Curator of the Jodrell Laboratory, to Mr. A. Gepp, Curator of the Cryptogamic Herbarium of the British Museum of Natural History, South Kensington, and to Mr. W. Emary for preparing the manuscript for publication.

The genus *Selaginella* consisted in 1887 according to Baker (1) of 334 different species, in 1900 (*vide* Hieronymus (7) in Engler and Prantl, *Die Natürlichen Pflanzenfamilien*) of 559, and in 1910 (*vide* the present writer's (26) *Die Pflanzengattungen*) of 580 known species. Like the ferns, most species are adapted to moist, shady situations; the forests of the tropics and sub-tropics being unusually rich in various forms. About 6 per cent of the species, however, inhabit dry localities, such as deserts and rocks of the Old and New World. I found their geographical distribution closely associated with that of xerophytic ferns, as has been outlined by Christ (3), their main distribution being the semi-arid regions of Mexico, the South Western part of the United States (especially Texas, New Mexico, Arizona and California), South America, Arabia, South Africa, the Mediterranean and the deserts

of Asia and Australia. As outstanding localities may be considered rocky and sandy situations in the midst of a non-xerophytic flora; such as dry ridges and rock outcrops occurring near mesophytic forests, and sand barrens which may occur anywhere.

Although excellent work has been published on the anatomy and morphology of *Selaginella*, especially by Cornaille (4), Gibson (9, 10), Haberlandt (12), Mitchell (17), Seyd (21), and Treub (24), only Leclerc du Sablon (14) in 1889 and Wojinorvić (29) in 1890 have contributed toward the knowledge of the xerophytic *S. lepidophylla*, Spring. Since that time, very little has been done on the subject, and other xerophytic species have scarcely been studied from an anatomical and physiological standpoint; comparative studies with plants of the same species under different environment have never been undertaken, neither has a physiological-anatomical classification of the plants in question been made.

Comparing various species of xerophytic and hygrophytic Selaginellas one soon notices the very close proximity of the dorsal and ventral leaves in the former (Fig. I, 1, 4, 5, 6), and the distance between the succeeding leaves in most species of the latter (Fig. I, 3). Moreover there is a striking similarity in the size of leaves in all xerophytic species the author has worked with; the size of the dorsal leaves differs only very little from that of the ventral leaves, although they may have slightly different shapes (Fig. II, 1, 2, X, 1, 2). In all hygrophytic Selaginellas, on the other hand, the difference in size and shape of dorsal and ventral leaves is very marked (Fig. I, 3). The writer considers the similarity in size in leaves of the xerophytic species (Fig. I, 1, 4, 5, 6; II, 1, 2, 8, 9; X, 1, 2) to be of much importance from a photosynthetic standpoint, as will be shown later: under the influence of their extreme environment the ventral leaves contain but few chloroplasts. Most of the production of organic matter therefore, as far as the action of the light is concerned, has to take place in the green cells of the dorsal leaves; were these leaves several times smaller, as is the case with hygrophytic ones, an insufficient amount of organic food would be formed, threatening perhaps the existence of the species. It is suggested that this factor must have been effective at the time, hundreds of centuries ago, when xerophytic species of the type *S. lepidophylla*, originated from distinct heterophyllous hygrophytic or semi-hygrophytic forms; those adapted to arid or semi-arid situations being alone able to survive.

FIG. I. *Xerophytic species.* 1, *Selaginella pilifera* Mexican desert; 2, from shady and moisty greenhouse; 4, *S. Pringlei* from Mexican desert; 5, *S. rupincola* from Arizona desert; 6, *S. sanguinolenta* from Karrum Valley Afghanistan. *Hygrophytic species*; 3, *S. Galeottei* from shady and moist greenhouse.

Note similarity in size of leaves of xerophytic forms, and difference in size of dorsal and ventral leaves of the hygrophytic one.

One is able to arrange various xerophytic species, collected in different dry countries in three distinct physiological groups, as follows.

Group I. Plants with vertical leaves, all of the same size and shape. The apex of each leaf ends in a long awn containing no chloroplasts. The anatomical construction of stem and leaves is decidedly sclerotic. Species belonging to this group all belong to the sub-genus *Homœophyllum*, e.g., *S. rupestris*, (L.) Spring, growing in rocky places of the northern and southern temperate zone of the Old and New World; *S. rupincola*, Underw. on rocks in south-western United States and Mexico; *S. Watsoni*, Underw. from the mountains of Utah and California; *S. Bigelowii* Underw. reported from California; *S. extensa*, Underw. collected from Las Candas, Luis Potosi, Mexico; *S. Underwoodii* Hieron. from New Mexico; *S. densa* Rydl. from various parts of the Rocky Mountain States; *S. mutica*, D. C. Eaton, on cliffs in mountains of Colorado, Arizona and New Mexico; *S. Ridellii* van Es. from central and eastern Texas and probably also in southern Louisiana; *S. humifusa*, van Es. growing on dry sandy soils in central and south Florida; *S. funiformis*, van Es. from the sand dunes and barrens of Florida; *S. tortipila*, A. Br. from South Carolina, growing on granite rocks in the mountains; *S. Sherwoodii*, Underw. growing on rocky places in North Carolina; *S. acanthonota*, Underw. growing on sand barrens in Florida, Georgia and North Carolina; *S. arenicola*, Underw. on dry sandy ground and rock waste of central and north Georgia and Florida; *S. caffrorum*, Hieron. and *S. capensis*, Hieron. reported from dry places in South Africa; *S. Mildei*, Hieron. from similar places in the province San Luis, Argentine; *S. Sellowii*, Hieron. from S. Diego, Brazil. There are further some other species belonging to this group, most of them being segregated from *S. rupestris*, of which many have been described by Hieronymus, Underwood (26), and Van Eseltine (8).

Group II. Plants having slender, wiry, trailing stems, spreading over the ground, or hanging down from rocks or sometimes from trees; the foliage consisting of two rows of dorsal and two rows of ventral leaves; the size of leaves being very much alike, although the shape may differ. Leaves of some species fold themselves round the stem when dry; certain forms have a slight resemblance to the last group; e.g., *S. sanguinolenta*, Spring from

rocky situations in Afghanistan and Eastern Siberia; *S. mongholica*, Rupr. from North China; *S. borealis*, Spring from Eastern Siberia, Kamschatka and Eastern Himalaya; *S. saccharata*, A. Br. from rocky, exposed situations in Mexico.

Group III. Plants having a spreading habit, stems often forming a flat, dense and close rosette; rolling into a nest-ball during drought. To this group belong *S. pilifera*, A. Br. growing in dry, rocky places in Texas, Southern Arizona and various parts of Mexico; *S. lepidophylla*, A. Br. from similar localities in Texas, New Mexico, Southern California, and from Mexico to Peru; *S. Pringlei*, Baker, from similar places in Texas and Mexico; *S. convoluta*, Spring growing in exposed places in tropical America from Mexico to Southern Brazil; *S. longispicata*, Underw. being reported from Yucatan, Mexico; *S. cuspidata*, Link. from Cuba, Mexico, Guatemala, and Venezuela; *S. imbricata*, Spring in semi-arid localities in Arabia, Abyssinia and Zambesiland; *S. involvens*, Spring from similar places in China, Japan, Amurland, Corea, and Eastern Himalayas.

Group I.

I was able to study *S. rupincola*, in its natural state in various parts of Southern Arizona (Sabino Cañon, Aqua Caliente and Oracle near Tucson) and *S. rupestris*, in Southern Arizona (Sabino Cañon, near Tucson) Southern California (San Bernardino Mountains) and various parts of the Ozark Mountains in South Eastern Missouri. Both species are petrophilous, growing mainly on exposed cliffs and rock outcrops. Individual plants on northern and north eastern exposures are well developed, their stems and leaves being greyish green and containing living protoplasm during the entire year. The few individuals on hot southern and south-western exposures are as a rule poorly developed; during the hot spells in summer the stems and leaves are entirely yellow or yellow brown, the protoplasm being killed. It is only during the rainy season that young shoots appear, which moreover never attain the same development as those on plants growing in favourable shady situations. Of both species the stems are densely tufted, ascending or decumbent; the leaves stand vertically close to the stem. They are all alike, sessile and possessing a groove in the midrib on the dorsal side; the margins bear one-celled bristles; the apex ends in a long awn and the sporophylls form terminal, somewhat four-angled spikes. The first thing one observes about *S. rupincola* is the vertical direction of the leaves, which are

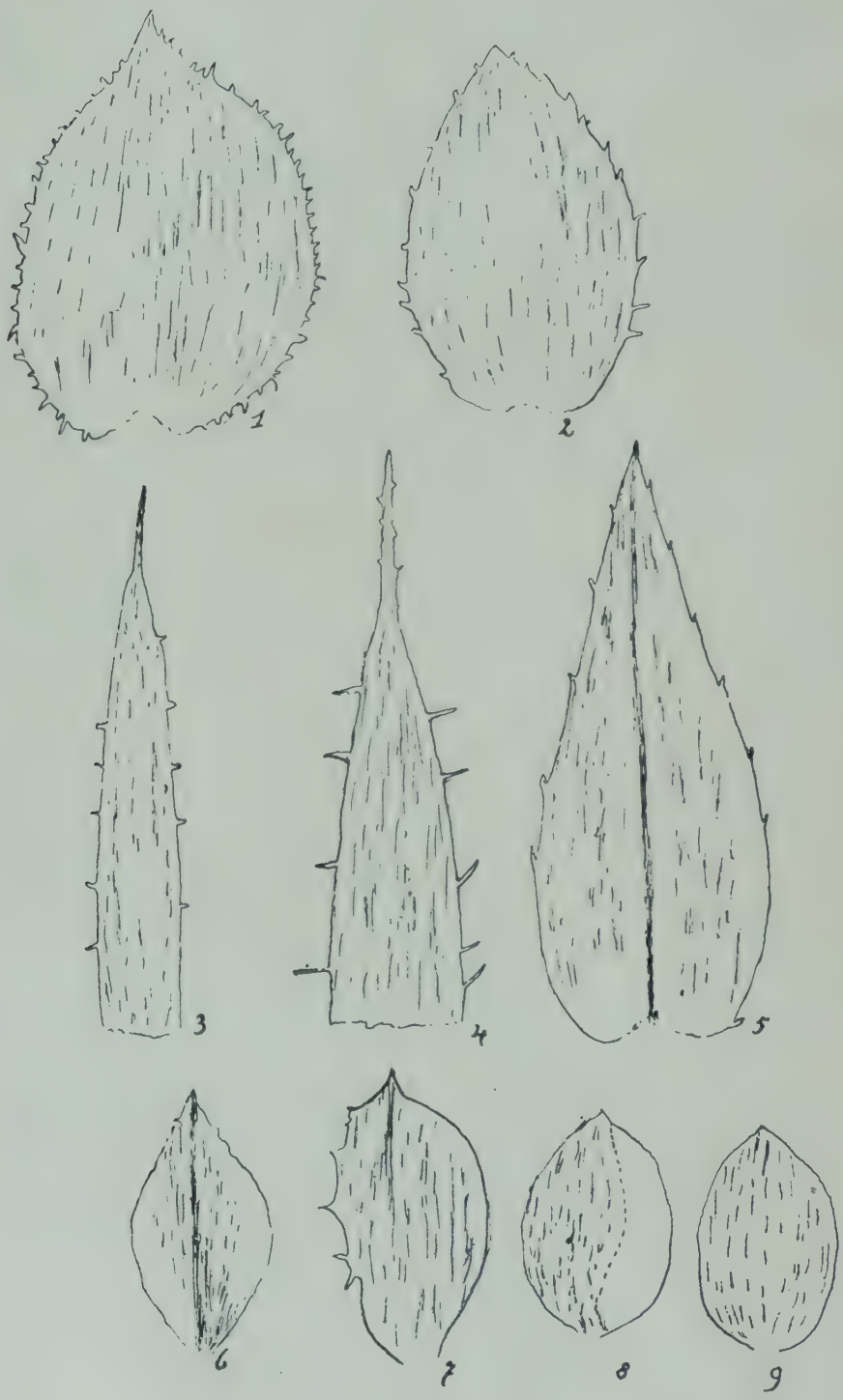

FIG. II. 1, 2, ventral and dorsal leaf of *Selaginella pilifera*; 3, *S. rupincola*; 4, *S. arenicola*; 5, *S. densa*; 6, *S. sanguinolenta*; 7, *S. borealis*; 8, 9, ventral and dorsal leaf of *S. saccharata*.

practically parallel with the stem. Only during the very hot summer when the temperature rises as high as 41·5° in the sun and 30° in the shade, can one recognise the advantage of this feature, when during the hottest hours of the day the sun's rays fall parallel with the leaves, whereas if the leaves stood horizontally they would be exposed to the perpendicular incidence of the rays. Further, one observes that the greyish-blue cuticle of the epidermis reflects the light to a certain extent, although this feature is not so marked as in the species of Group III. The growing point is protected by a close bundle of long awns on the young leaves surrounding the apex of the stem. The cells of these awns are elongated, thick-walled and entirely destitute of chlorophyll, reflecting almost all the light falling upon them (Fig. I, 5 ; II, 3, 4, 5 ; III, 9 ; V, 5). The same feature can be observed in all the species belonging to this group. Awns on leaves of older and lower parts of the stem do not seem to be of great importance, as a protection from the sun, but they retain the power of reflecting light. In *S. densa* the leaves are broader than those of other species (Fig. II, 5), and are folded length-wise round the stem, the halves being almost at right angles to each other, and lying very close against the stem. This structure and position of the leaves minimises transpiration. *S. densa* was collected in a dry pine wood in Dappatah, Florida. The same conditions exist in psammophilous species, *i.e.*, those found in sandy soils, which are for a large part of the year physically dry, on account of the rapid drainage of water after rains. Species from such localities are *S. arenicola*, *S. funiformis*, *S. acanthonota* and others.

Sections of various parts of plants of this group exhibit a very sclerotic anatomical structure. A section of the stem (Fig. III, 6), of *S. rupestris*, collected on an exposed granite rock near Sabino Cañon, shows a very thick cuticle; the cell cavities of the epidermis being very small, on account of the secondary layers of the walls. The hypodermis is usually composed of three rows of cells of the same size as those of the epidermis. The cells of the cortex are larger, and the walls become gradually thinner as one proceeds further into the plant, although they are never as thin as those of hygrophytic forms. In thin sections one readily finds in the thick walls layers and remains of plasmodesmi. The protoplasm of the epidermis, hypodermis and outer cortical cells very soon dies, after the secondary wall layers are formed. In very young tissues these cells sometimes contain a few chloroplasts,

especially the future thick-walled outer cortex, at a later age only the thin-walled inner cortex contains living protoplasm with a few chloroplasts. At first, when very young, these cortical cells contain small intercellular spaces, but these soon disappear. The vascular bundle, which is in all species simple, contains a well developed phloem; the cells of the pericycle are relatively large, the cells of the protophloem, sieve tubes and phloem parenchyma are smaller. The vessels of the protoxylem and metaxylem are considerably narrower than those of the hygrophytic forms, owing to the reduced water supply of the plants.

The cross section of a leaf (Fig. III, 7, V, 1, 7), is somewhat boat-shaped, the epidermis is thick-walled, covered by a thick cuticle. The wings of the leaf contain a thick sclerotic tissue, composed of two, sometimes of four, layers. The mesophyll is everywhere surrounded by the thick cells mentioned above; the air-spaces between the cells are small, except where stomata occur in the groove along the midrib of the aligular surface, and here the air-spaces become much larger. The stomata are protected by a very thick cuticle (Fig. III, 3), which contains opposite the entrance of each stomata, a small air chamber, leading through a narrower passage to the guard cells.

The contrast in development of tissues between plants from very dry and exposed situations, and individuals of the same species from a moist and shaded greenhouse at Kew is striking (Fig. III, 1-10). The adaptation of such xerophytic forms to a pure hygrophytic environment manifests itself at once. Plants from the latter possess almost horizontally placed leaves, instead of vertical ones (Fig. III, 5, 10). The leaf surface does not reflect the light: the awn at the apex of the leaf is considerably shorter in comparison with that of the desert type (Fig. III, 4, 9); it has entirely lost its purpose, although it is composed of sclerotic elongated cells. The sporophylls, which form a four-sided spike, lie closer against the axis of plants from dry environments, protecting the mega-and microsporangia, than is the case with the sporophylls developed in a moist environment.

A cross section of the stem (Fig. III), of the same age, shows a thinner cuticle; the cell cavities of the epidermis and of the hypodermis are larger, because the cell-walls are thinner. All the walls of the cortex are considerably thinner, and the cortical cells possess living protoplasm with 4 to 5 chloroplasts. An important feature of the vascular bundle is the greater width of the vessels in

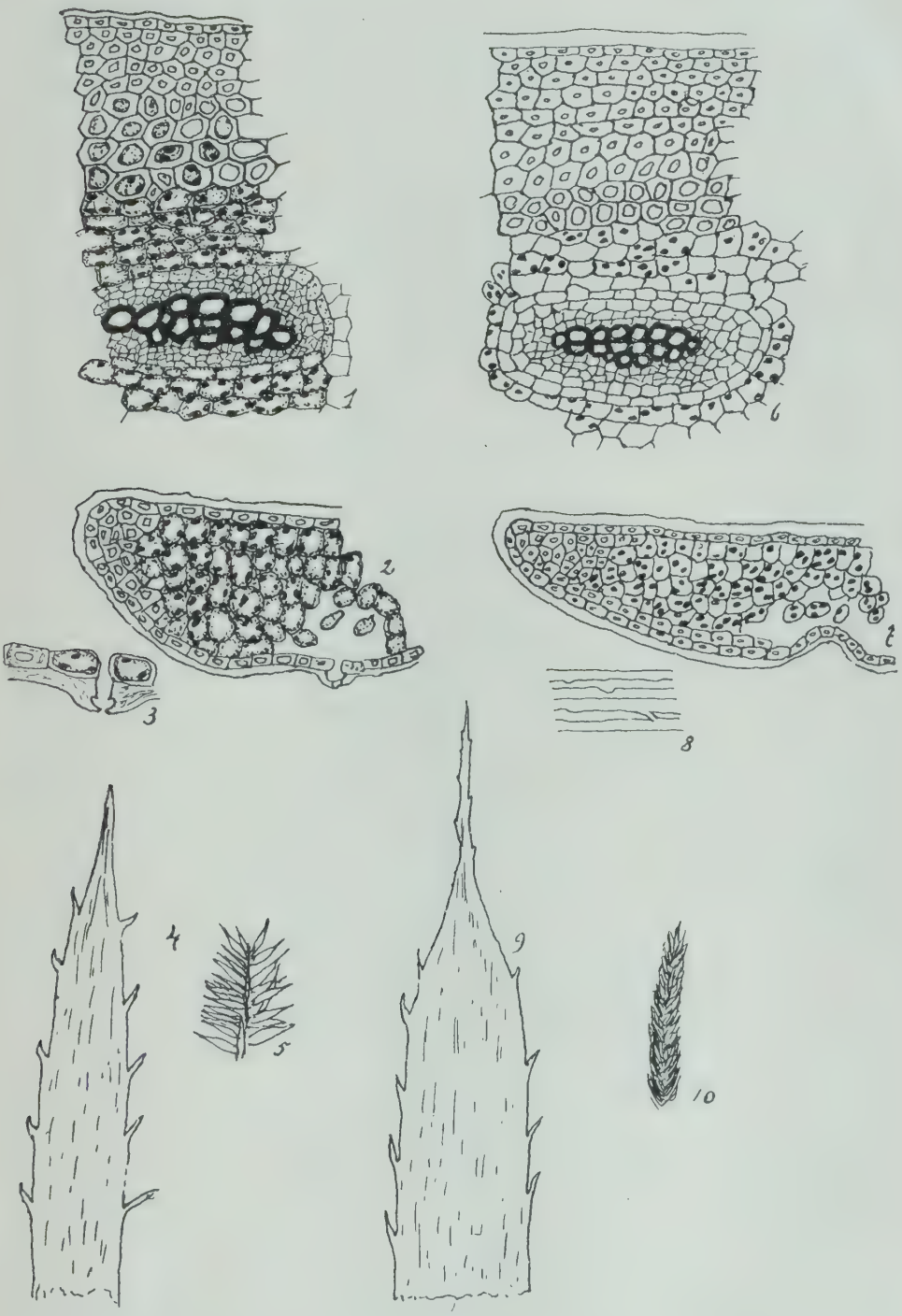

FIG. III. *Selaginella rupestris.* 1, section of stem; 2, section of leaf; 3, stomata; 4, leaf; 5, habit of plant. All developed in shady and moist greenhouse; 6, section of stem; 7, section of leaf; 8, sclerenchyma of leaf; 9, leaf; 10, habit of plant. All developed in semi-arid desert.

the xylem, because the water supply has increased; although they are never as wide as those of hygrophytic Selaginellas. The difference in size of the elements of the phloem is not considerably marked. A section of the leaf (Fig. III, 2), shows a somewhat thinner cuticle; the stomata, which also only appear in the groove on the aligular face, are present in larger number, their guard cells are covered by a thinner cuticle; although the external air chamber remains. The sclerotic cells are not as numerous, and not as thick. The cells of the mesophyll are slightly larger and have broader air spaces between them; those toward the stomata are considerably larger.

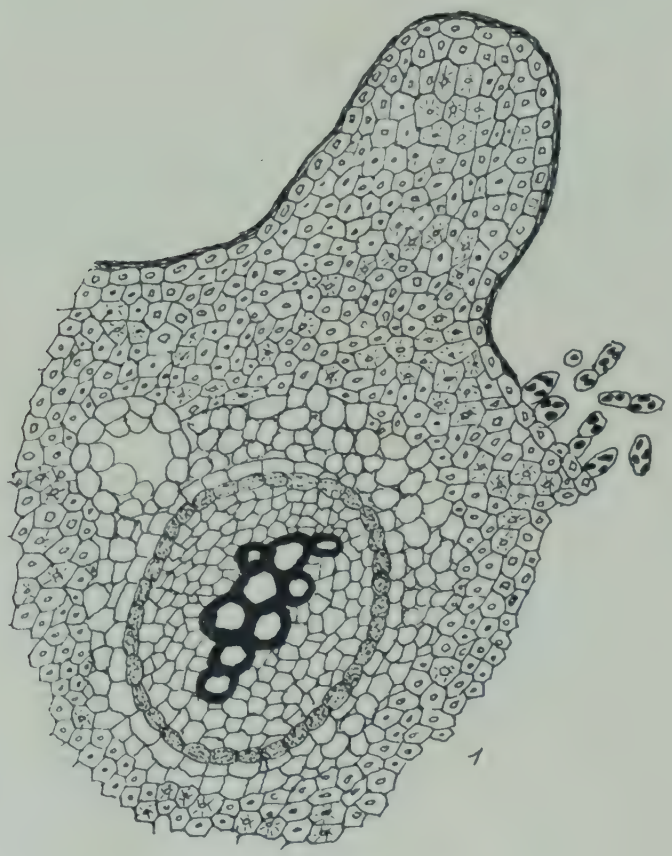

FIG. IV. Selaginella arenicola, section of stem.

Treatment with KOH shows that all the thick-walled tissues are heavily suberized in those plants grown in exposed places. The yellow color is not as intense in tissues of plants grown in the moist environment of the greenhouse, which suggests a less amount of suberine in the secondary walls. The awns and the wings of the leaves, composed of sclerotic cells, are suberised.

Selaginella arenicola, a psammophilous species, collected from a dry, sandy pinewood near Dappatah, Florida, shows a similar anatomical construction, the hypodermis, however, is thicker along certain radii of the stem, giving an irregular star-shaped form on a cross section (Fig. IV), on the other hand the stem of *S. rupestris* has a square, sometimes a five-angled shape. Old cell walls which were very exposed are impregnated with a red-brown pigment, which, no doubt, serves as a protection against very intense light. The vascular bundle of the stem shows the same characteristics as in *S. rupestris*, *S. rupincola* and *S. densa*. A cross section of the leaf shows a far more developed sclerenchyma than in the species previously described (Fig. V, 1). The stomata, which also appear on the aligular surface, are protected by stiff one-celled hairs. On a longitudinal section of the leaf (Fig. V, 6), one notices the thick-walled elongated cells of the sclerenchyma. The mesophyll contains larger inter-cellular species than in the species previously described; it is composed of roundish cells toward the upper surface, lower down they are elongated.

A section of the leaf of *S. rupincola* (Fig. V, 7) is of much the same structure as *S. rupestris*. The vascular bundles in the leaves of all species mentioned under Group I, are best developed near the base and occupy only a small portion of the centre of the leaf. The bundles are usually composed of four narrow tracheids, which are narrower than those of plants developed in a moist situation. Around the xylem are some parenchyma cells and a few sieve tubes, which do not show any differences in plants grown in various environments.

Group II.

Plants belonging to this group have a flat, spreading habit and have slender stems which are as a rule widely branched, and wholly or partly covered with small, sometimes scale-like, leaves. Some species show resemblances to the third group, as they are able to roll up during drought, but do not form a nest-ball, since they are too widely branched. One of the principal representatives is *S. sanguinolenta*. The plant examined was collected in a rocky mountainous situation in Kurram Valley, Afghanistan. The stem is very thin, spreading and pinnately branched; and the branches frequently sub-divided again; these divisions are short and covered with very small scale-like leaves (Fig. I, 6) all of the same size and shape. This species is supposed to stand near the borderline of the heterophyllous and homophyllous Selaginellas. These leaves are

convex on the aligular surface, consequently the ligular surface is concave and partly surrounds the stem; their shape is oblong, obtuse, about 0·7 to 1 mm. long (Fig. II, 6). Old parts of the stem are leafless, and possess a bright red color. There is a very thick cuticle, the cells of the epidermis, hypodermis and outer cortex, which are very thick-walled, do not show difference in size (Fig VI, 1). The inner cells of the cortex are thinner walled, retain their protoplasm longer and possess 4 to (sometimes) 6 chloroplasts. I was unable to find intercellular spaces, excepting in a few cases in very young tissues. With age the space in the thick walled cells

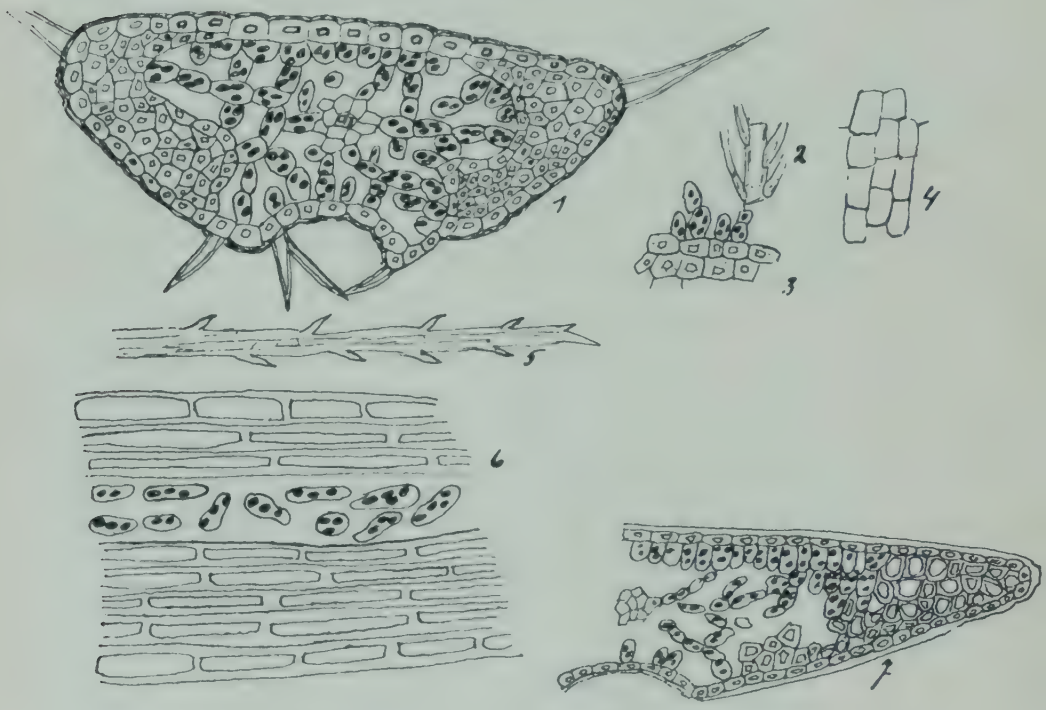

FIG. V. *Selaginella arenicola*. 1, section of leaf; 2, attachment of leaves to the stem; 3, base of leaf and part of stem; 4, part of epidermis of stem: 5, awn at apex of leaf; 6, longitudinal section of wing of leaf *rupincola*; 7, cross section of leaf.

becomes very small, through formation of secondary wall layers; all the walls are impregnated with a red or brown-red pigment, which serves as protection against intense sun's rays. Toward the vascular bundle, there is a wide sharply defined lacuna and the trabeculæ consist of narrow cells, which later sometimes divide into two. The spaces in this tissue are large, while they are absent in the plants of Group I. The elements of the meta- and protoxylem are narrower than in any xerophytic species the writer has worked with and stand in close relation with the low water requirements and supply of the small leaves. The different parts of the phloem are

all present, the cells of the one layered pericycle are relatively larger.

The leaves show on cross section a very thick cuticle, and thick epidermis cells; no sclerenchymatous tissue is developed. The mesophyll shows rather a hygrophytic character; it is composed of one layer of palisade cells, and a strongly developed spongy parenchyma, with large air spaces throughout the entire tissue (Fig. VI, 3). The stomata, which occur on both aligular and ligular surfaces, are small, and protected by a very thick layer of cuticle. The wings of the leaves are composed of thick-walled mesophyll cells which are formed close to each other, and apparently do not possess intercellular spaces.

The other species studied was *S. saccharata*, collected on bluffs near Guadalajara, Mexico. Its stems are trailing and pinnately branched. There is but little difference in the size of the leaves (Fig. II, 8, 9), which are 0·75 to 1 mm. long, the dorsal leaves of some individual plants are slightly shorter than the ventral leaves, and are pale green. The leaves of the lower plane are white when dry, reflecting the light to a considerable extent. When growing exposed to intense sun they become brown or red brown, the pigment occurring only in the cell walls, especially in the lower epidermis. During drought the younger parts of the stems curl up to such an extent that parts of the lower surface of the stem and leaves lie in the same direction as the upper surface, thus covering and protecting the true upper side of the plant against drought, heat and extreme light.

A cross section of the stem shows a thick-walled epidermis, its cuticle being especially strongly developed. The thick-walled cells of the hypodermis differ but slightly from those of the epidermis; the cells of the cortex are larger and thin toward the vascular bundle. There is a striking difference in thickness between the cortex cell walls of the uppermost part of each branch and that of the lower surface; in the former they are thin-walled, in the latter thick-walled. The difference stands in close relation to the curling movement of the branches when the plant becomes dry: this will be fully considered and explained in dealing with the species of Group III. All the cells of the cortex contain in their youth chloroplasts and air-spaces, but these disappear in the thick-walled tissues of the outer cortex. The tracheids of the xylem are narrow.

The leaves (Fig. VI, 4, 5), possess a thick-walled epidermis; the mesophyll is composed of a one celled layer of palisade parenchyma; the cells of the sponge parenchyma have the same shape as those of the palisade; the intercellular spaces are small, though distinct.

The writer regrets he was unable to study any of the plants of this group under natural conditions. The habitats of these plants, which differ widely from those of the other two groups, must have an effect on their development and behaviour, and these facts can only be satisfactorily studied in their native environment.

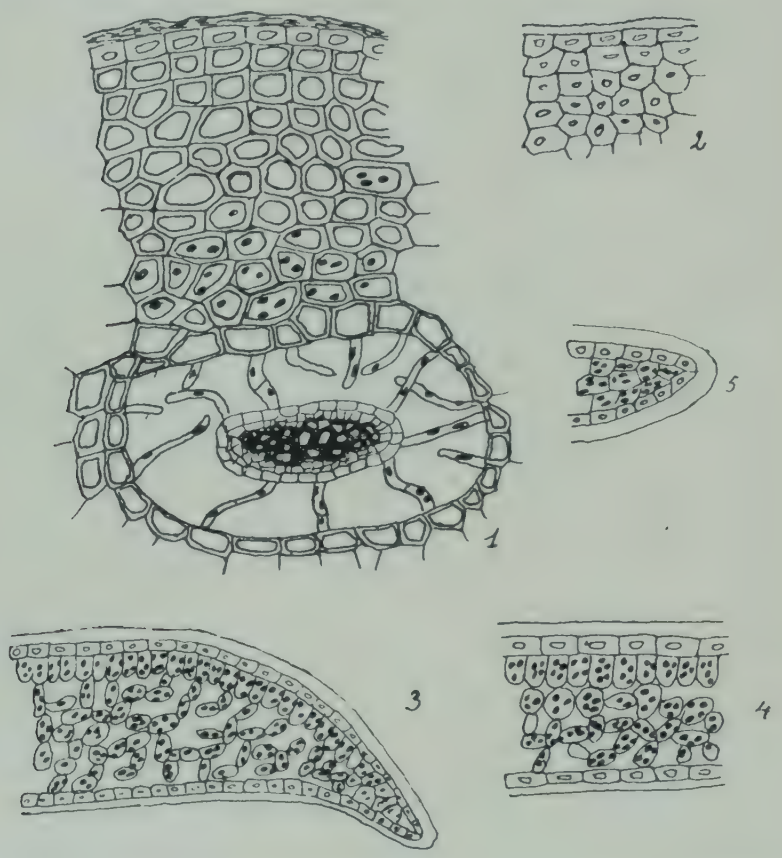

FIG. VI. *Selaginella sanguinolenta*. 1, section of leafy stem; 2, section of old leafless stem; 3, section of leaf. *Selaginella saccharata*; 4, 5, sections of leaf.

GROUP III.

Plants of the last group are exceedingly well fitted for a semi-arid environment. The stems are densely tufted, and curl up into a more or less close cluster; the leaves are situated horizontally on both sides of the stem; the dorsal leaves are only a little smaller than the ventral ones. The under sides of the ventral leaves, which become the outside of the cluster when curled up during drought, reflect much of the light they receive. The cells contain a large amount of oil. They form the series *Rosulatæ* of Baker (1).

The writer was able to study plants in their natural state, especially *S. lepidophylla* in Southern California (environs of San Diego), and Northern Sonora, Mexico (a few miles from Los Nogales); *S. pilifera* also was studied near Los Nogales.

Both species prefer exposed, rocky situations, especially with a northern aspect. In the neighbouring flat rockless deserts they are never met with. The plants are subject to extreme drought and intense heat; for a large part of the year under such circumstances they are to be found curled up into a big loose cluster-ball; the underside of the plant, which is alone exposed, differs in color in proportion to the amount of its exposure to the full severity of the sun. When not so exposed, owing to protection by the shadow of big rocks, this underside is almost white; the stronger the effect of the rays on the plants, the more the underside of the leaves will contain a brown to red-brown color. When illuminated by the sun's rays, the clusters appear to be more or less glossy on account of the light being reflected by the white or brownish cells. The clusters are sometimes detected with difficulty at small distances on account of the similar color of surrounding rocks and are thus easily overlooked.

The air temperature, the rainfall and relative humidity to which the species of this group are especially subject are of much importance. It is therefore necessary to give meteorological data, partly collected by the writer in the neighbourhood of Tucson, Arizona, which is under much the same weather conditions as the neighbourhood of Los Nogales, Mexico.

Air Temperature, 5 c.m. above the ground at Tucson, Arizona—Altitude 723 metres,

Month.	Temp. in Sun °C.	Temp. in Shade °C.	Month.	Temp. in Sun °C.	Temp. in Shade °C.
January ...	18·5	12·5	June ...	35·0	25·0
February ...	24·7	15·0	July ...	38·2	26·1
April ...	30·2	20·1	August ...	41·5	30·2
May	27·3	22·0	September ...	39·0	25·5

The annual rainfall in different sections of Southern Arizona, varies with the altitude, as may be seen from the following figures; the rainy season at lower elevations is in winter.

Name of Place.	Elevation in Metres.	Summer rain in Millimetres.	Winter rain in Millimetres.	Annual rainfall in Millimetres.
Yuma ...	45	10	51	78
Maricopa ...	351	45	78	143
Casa Grande	711	40	71	130
Tucson ...	723	134	114	274
Oracle ...	1440	182	215	449

The relative humidity differs greatly, not only with the time of year, but also at different parts of the day. On very hot days at about 2 p.m. it ranges from 25 to 35, between 5 and 6 a.m. from 80 to 90, at 10 p.m. from 35 to 50. The number of cloudless days during the year is considerable, amounting to over 320.

Meteorological conditions of semi-arid regions in the Old World are similar to those in Southern Arizona. As the xerophytic plants which the author has studied are also to be found in dry regions of Asia and Africa, it is useful to give data relating to these parts of the world as far as could be obtained. Most of the data were obtained from the *Meteorologische Zeitschrift.*

Temperature, Relative Humidity and Rainfall of various Deserts.

Month.	North Africa and South West Asia.			Algerian Sahara.			West Central China.			South African Desert.		
	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.	Max. Temp. Centigr.	Relative Humidity.	Rainfall mm.
Jan.	24·8	81·5	44·8	20·7	48	19	10·5	82	18	21·7	90	1·1
Feb.	29·8	86·0	19·0	23·8	31	7	14·0	57	0	23·9	92	1·6
Mar.	20·2	83·0	8·1	30·7	26	15	24·5	65	23	29·4	92	3·2
April	20·1	83·0	7·1	34·3	21	8	33·7	40	13	34·4	84	5·0
May	20·2	92·0	0	39·0	17	17	35·7	25	13	33·3	90	14·5
June	22·9	91·0	0	45·1	14	1	38·2	19	0	28·3	86	7·9
July	22·3	93·0	0	47·4	12	0	40·5	29	5	25·6	88	5·2
Aug.	26·7	94·0	0	46·6	15	2	35·5	30	6	26·1	87	6·8
Sept.	28·7	92·0	34·7	42·6	19	4	36·1	26	0	39·4	79	5·6
Oct.	25·9	92·0	55·9	36·7	31	3	21·9	35	0	32·8	76	2·8
Nov.	25·7	89·0	38 1	27·1	37	10	22·0	39	1	37·2	80	2·2
Dec.	25·0	87·0	17·3	21·1	45	28	17·7	67	10	38·3	88	1·1
Whole Year			225			114			89			57

The reflection of light from the underside of a leaf of *S. pilifera* or *S. lepidophylla*, as seen under the low power of the microscope, is confined to the ventral leaves. Chlorophyll and living protoplasm are absent, the cells are colorless, with the exception of these cell-groups exposed to the extreme action of the sun, which have their walls impregnated with a red-brown pigment. Only small sections which are covered by a part of the succeeding leaf remain green and are alive. In their natural environment the ventral leaves become mainly agents of reflecting light, instead of producing organic compounds under influence of the light. This production is taken over by the entirely green dorsal leaves, which explains their being in comparison to the ventral leaves much larger than those of the hygrophytic species. Fig. IX, 1, 2 shows a

part of the underside of a ventral leaf; (a) being very much exposed to the sun's rays has a red-brown color; (b) which was less exposed is white and glossy, both (a) and (b) reflecting the light; (c) remains green having been deeply shaded by a part of the next leaf, and possesses living protoplasm. A cross section of the leaf shows that none of the tissues under (a) and (b) contain any chloroplasts, only some grayish bodies in the cells which may indicate their presence at an earlier stage of development; very young leaves which are developed during the rainy season are

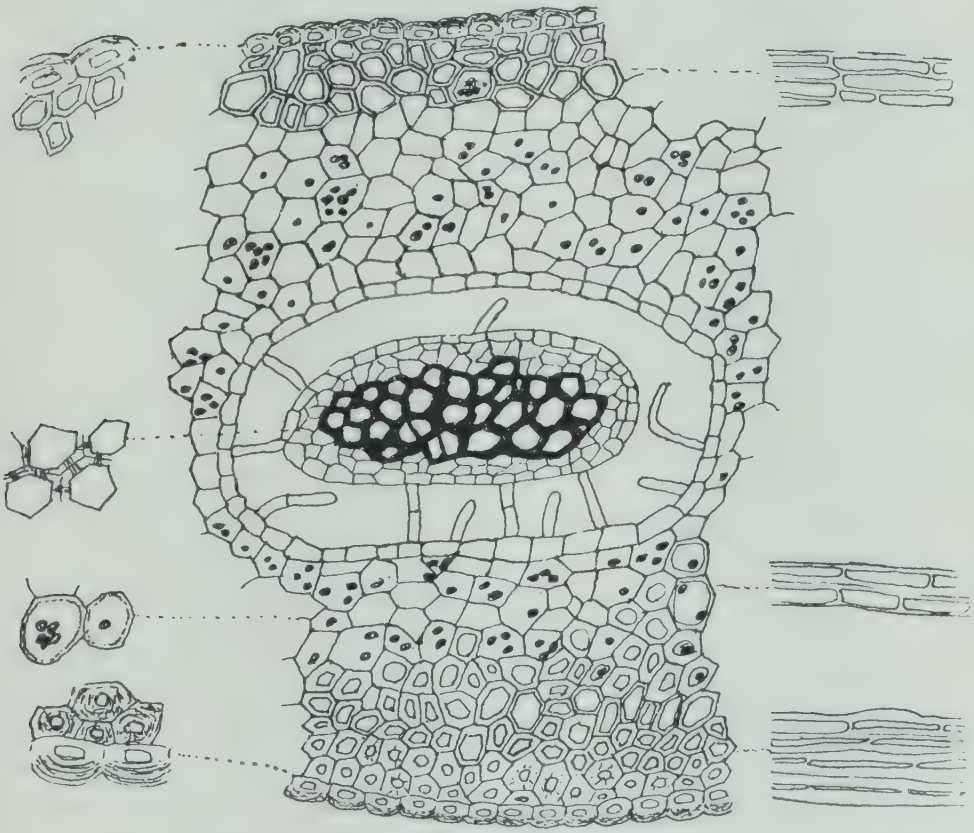

FIG. VII. Section of stem of *Selaginella pilifera* from moist and shady greenhouse. Note difference of cell walls of upper and lower surface.

entirely green. These chloroplasts must have been destroyed by the intense light; thus if parts of leaves which shade green portions of the succeeding leaf are removed, after a short time the exposed parts also become colorless and soon light reflecting.

Leaves of plants developed in a moist and shaded greenhouse are entirely green, with the exception of two rows of cells on the margin which are colorless.

Moreover the writer found on desert plants which are very much exposed that the underside is covered with a hard translucent

colloidal layer, which contributes very much towards its protection from extreme transpiration ; plants from more favourable situations do not possess such a layer. This can easily be detected with low powers of the microscope, and readily removed from the underside of the ventral leaves, clearly showing the imprints of the elongated cells of the epidermis. In contact with water the colloidal layer very quickly absorbs the liquid, losing the cell imprints, increasing five to six times in size, and slowly forms a structureless gelatinous substance. The colloid absorbs a weak solution of eosin, staining red in a short time, while the surrounding water remains pink. Water evaporates more slow from this gelatinous matter than pure water would do. This fact can be readily observed on the plant. There is no doubt that the colloidal layer has two functions to perform; in the first place it protects the plant against extreme heat, through minimizing transpiration by covering such parts of the plants by a hard substance; in the second place it absorbs the water after a shower or heavy dew and retains it longer than if the plant were without the gelatinous cover. The thickness of this colloidal layer, when dry, is sometimes thrice that of the leaf which it covers.

In *S. lepidophylla*, the chlorophyll-free margins of the dorsal leaves toward the apex are broad (Fig. X. 3) and reflect the light; the author observed that this is of much importance during the early development of the young dorsal leaves toward the growing point of the stem, since each half developed leaf is protected against the light by the broad margin of its neighbouring leaf. This feature is only of use when the branches are spreading in a horizontal direction, as they do when moistened.

The leaves of *S. Pringlei* have instead of a broad chlorophyll-free margin, a long awn at the apex (Fig. X, 1, 2) ; when the leaves are young, the awns of several leaves are situated close to each other toward the top of the shoot (Fig. I, 4), thus protecting the very young leaves. Also the growing point of the main stem, in the centre of the plant, is thus thoroughly protected by the awns. At a later stage the awns become valueless.

When it rains the cluster-balls soon unfold. This movement manifests itself in 1 to 2 hours, the whole plant becoming a flat rosette in 10 to 12 hours. The absorption of water by the tissues increases the weight of the plant by approximately 50 per cent, as is shown from the following table.

Increase in Weight due to absorption-water after moistening for two hours.

	Condition	Increase of weight		Condition	Increase of weight
S. lepidophylla	dead	48·6%	*S. convoluta*	dead	54·0%
S. lepidophylla	living	51·0%	*S. imbricata*	dead	52·5%
S. pilifera	dead	42·0%	*S. Pringlei*	dead	51·0%
S. pilifera	living	45·0%	*S. longispicata*	dead	47·2%
S. cuspidata	dead	43·4%	*S. longispicata*	dead old stem	40·0%
S. cuspidata	living	46·0%	*S. involvens*	dead	47·2%

Shoot apices (including fully developed shoot) 15 mm. in length were used for these experiments. An old stem of *S. longispicata* of the same length showed a slightly smaller increase. It will be seen that living plants absorb slightly more water than dead plants.

The morphological and anatomical structure, especially of *S. lepidophylla* has been frequently discussed, *e.g.* by Hieronymus in Engler and Prantl "Die Natürliche Pflanzenfamilien" (7), Lotsy (15), Neger (18), and others. Original investigations were conducted by Leclerc du Sablon (14) and especially by Wojinorvić (29). I have carefully examined the work of the two last authors and compared their results with related species. Some of the results are correct, but other very important deductions have proved to be misconceptions.

Wojinorvić states that the main axis of *S. lepidophylla* has a spiral form, due to a different development of one of the two shoots. This interesting account, can only be expressed to the best advantage in his own words: "Die Entstehung dieser eigentümliche Form der Axe ist morphologisch so zu erklären, dass am Vegetationspunkte dichotomisch zwei Aeste angelegt werden, von denen der Rechte kräftiger wächst und strahlenförmig nach Aussen abliegend, als Seitenzweig auftritt, der Linke dagegen stellt die Verlängerung der Stammesspitze dar und wachst, nicht in derselbe Ebene bleibend, langsam nach oben, indem er sich dabei gleichzeitig spiralig nach innen dreht."

Through repetition of this kind of growth, as explained above, the peculiar spiral arrangement of twigs round the axis takes place. I clearly observed the same principle in other Selaginellas, e.g., *S. pilifera*, *S. Pringlei*, *S. involvens*, *S. cuspidata*, and *S. longispicata*, but was unable to find this development in *S. imbricata*. This characteristic seems peculiar to these species of Selaginella and has not been observed in other plants.

To explain the hygrochastic movement of the stem it is necessary to understand the anatomical structure. Leclerc du Sablon (14) states it is due to a difference in thickness in the cell walls on the two sides of the stem; the upper side, he says, is thick-walled, the lower thin-walled. Wojinorvić (29) is of the same opinion: "Die organisch Obere, bei der Zusammenrollung der Pflanze einwärts gekrümmte und daher concav werdende Seite wird aus Zellen mit stärken verdickten Wänden gebildet als die organisch Untere, bei der Zusammenrollung äussere, also convex werdende

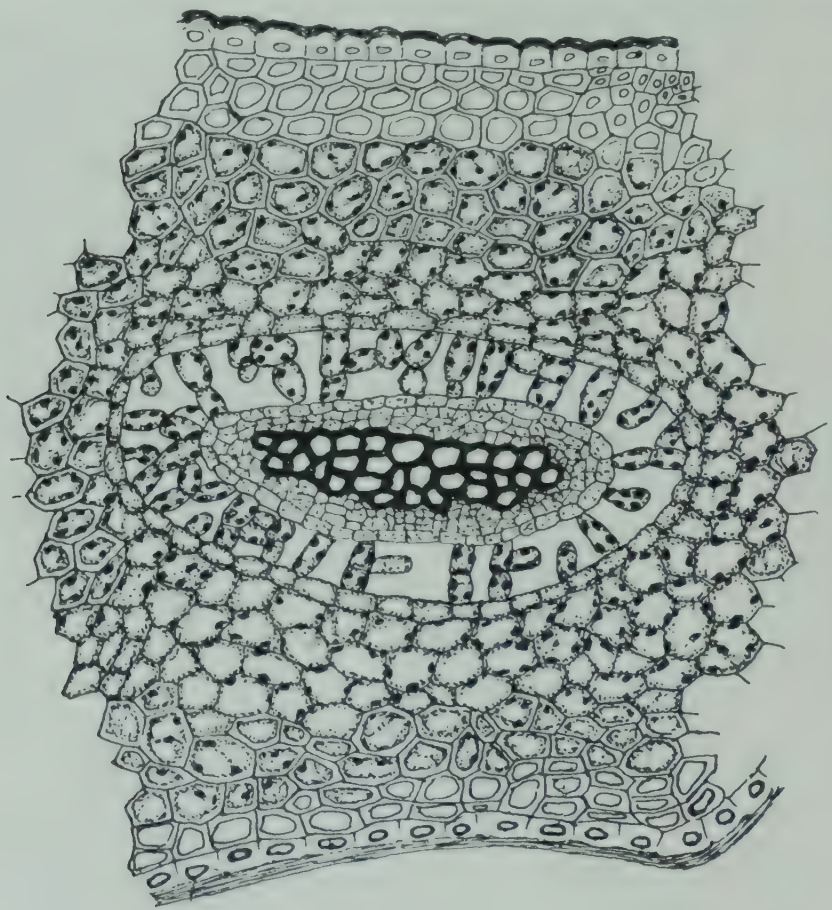

FIG. VIII. Section of stem of *Selaginella pilifera* from moist and shady greenhouse. Note similarity of cell walls of upper and lower surface.

Seite." He states further that the thick-walled cells absorb more water than the thin-walled ones and the former lose more water during drought than the latter, causing the plant to curl up and to have the appearance of a cluster-ball.

I found after careful examination that the tissues are neither thicker-walled on the upper nor thinner-walled on the lower side of the stem, but precisely the reverse and also that the thin-walled

tissue absorbs more water than the thick-walled. A close observation of transverse and longitudinal sections of the stem of *S. cuspidata*, *S. pilifera* (Fig. VII), *S. lepidophylla*, *S. Pringlei*, and *S. longispicata* from extremely exposed situations shows that on one side of the stem the cell walls are deep red brown and on the other side of the stem the cell walls are colorless; the ventral leaves are also partly brown or red brown, while the dorsal leaves are green. On longitudinal sections the red brown cells of one half of the stem are easily seen to be on the same side as the red brown celled leaves; on the other hand the colorless part of the stem carries the green leaves. On cross section it is at once evident that the colorless part is thin-walled and the red brown part of the stem is thick-walled. Consequently the former belongs to the uppermost part of the stem, the latter forming the lower surface of the stem.

The thick-walled cells are to be found in the epidermis, hypodermis and the outer cortex; the room in the cells is very much reduced; the walls clearly show secondary layers; the inner cortex is thinner-walled. When the stem becomes older, the whole of the inner cortex also becomes very thickwalled, with the exception of about two rows of cells toward the bundle. The epidermis of the upper side is almost as thick as that of the lower surface, but the cell walls of the hypodermis and cortex are considerably thinner. Moreover the thick-walled cells are much more suberized than the thin-walled ones. It follows that the thin-walled upper surface loses more water during drought, and absorbs more when moistened than the thick-walled tissues of the lower surface, and that this causes a corresponding curling up and spreading out of the shoot.

When a longitudinal section of a stem is observed in water, the thick-walled and thin-walled tissues appear to be of the same length; when dry the thick-walled side is longer than the thin-walled one; a difference which is considerably more pronounced on gently heating on a glass plate above a flame. When water is added to the dry slide, it is at once noticeable under the microscope that the thin-walled tissues absorb much water and increase appreciably in length; the thick-walled tissues, on the other hand, which during drought were curved toward the thin-walled, absorb very little and are straightened out again by the increase in length of the thin-walled tissue. The length of the tissues when dry and when moistened are summarized in the following table:

Length in mm. of longitudinal sections of full-grown stems of xerophytic Selaginellas.

Name	Condition	Wet	Dry	
		Equal length of both tissues	Length of thick-walled tissues	Length of thin-walled tissues
S. pilifera	dead, from Mexico	·900	·885	·835
S. pilifera ...	living, from greenhouse	1·200	1·190	·1140
S. lepidophylla	dead, from Mexico	1·000	·985	·935
S. lepidophylla	living, from desert region	·900	·880	·820
S. cuspidata	dead, from Mexico	·900	·880	·825
S. cuspidata	living, from greenhouse	1·000	·975	·950
S. longispicata	dead, from Mexico	1·000	·975	·930
S. Pringlei	dead, from Mexico	·900	·885	·840

The movements of the tissues are entirely mechanical, as their cells when old do not contain living protoplasm even in living plants: moreover similar results are obtained in dead plants as is shown in the table. They depend upon the hygroscopic capacities of the tissues, being entirely physical instead of biophysical. After drying above a flame, the tissue soon absorbs moisture from the surrounding atmosphere in a damp climate.

In *S. pilifera* there is a well developed lacuna with well formed one or two-celled trabeculæ round the bundle; the trabeculæ are thinner in individuals grown in a moist and shady environment. The proto- and metaxylem is well developed, although in proportion to the water supply of the stem.

Plants which were grown in a Wardian case in a moist and shaded greenhouse at Kew show different structural characters. The leaves are further apart and do not lie so flat against the stem (Fig. I, 1, 2). The cell walls of the epidermis, hypodermis and cortex are considerably thinner; the cuticle however is only slightly thinner. There is not much difference in thickness of the walls between the tissues of the uppermost part and the lower surface; consequently the stems do not fold up so much when dry. The tissues of the lower part of the stem are not impregnated with red brown pigment. Moreover the presence of suberin is less pronounced than in plants grown in a semi-arid environment. The intercellular spaces are larger and persist longer in plants grown in the greenhouse; also protoplasm remains longer in the cells of

the hypodermis and cortex (Fig. VIII). The xylem is of the same width but its elements are more numerous.

A section of the desert-grown ventral leaf shows a considerable thickness in both cuticles, especially the parts directly exposed to the sun's rays; the epidermis is thick-walled. The same tissue of the plant from the greenhouse is thinner and contains less suberin; the mesophyll of the former is composed of oval cells with small intercellular spaces; thə mesophyll of the latter has larger air-spaces (Fig. IX, 2, 3). The stomata appear toward the middle of the

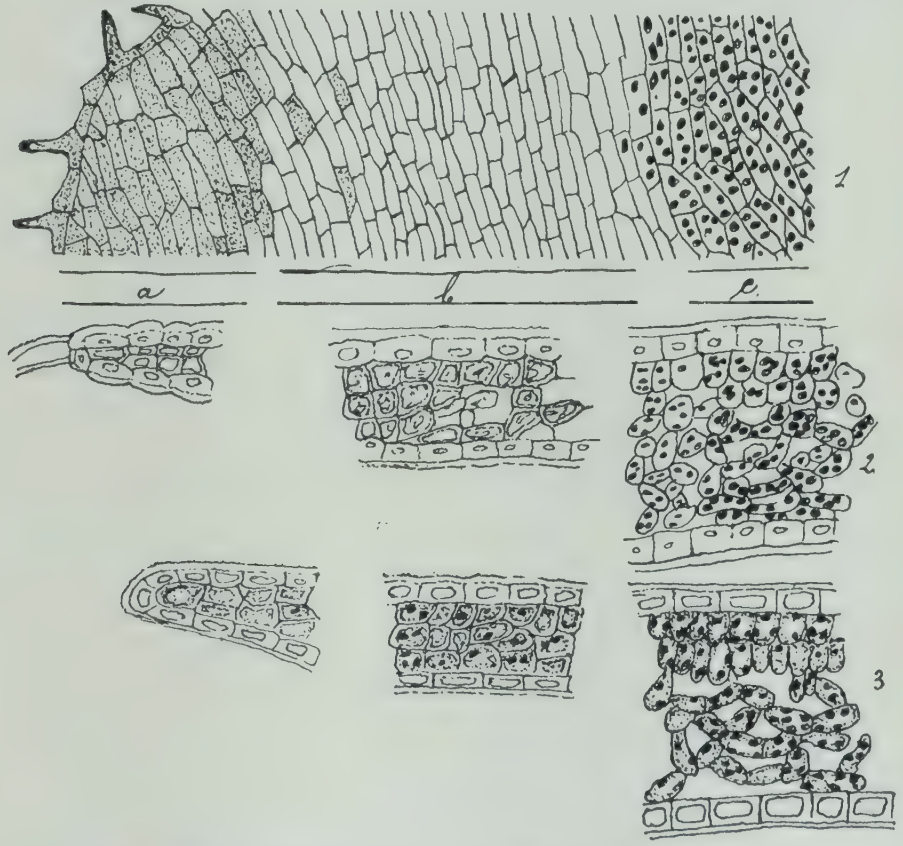

FIG. IX. Leaf of *Selaginella pilifera* 1, longitudinal view; 2, cross section; *a* and *b* exposed to intense sun's rays of which *a* has brown cell walls, only *c* has chloroplasts; 3, cross section of leaf developed in shade, all cells of mesophyll possess chloroplasts.

aligular side, being more numerous on a plant developed in the moisture. A very few stomata appear on the ligular surface of both kinds of leaves, although their influence upon transpiration and movement of gases can be but small. The cells toward the wings or margins of the leaf contain only one or two big chloroplasts, sometimes none, instead of 8 to 12 as in the other cells of the mesophyll. The dorsal leaves of both plants from the desert and from the greenhouse have a more pronounced spongy

parenchyma, which is thicker and here and there contains large air spaces. Although the anatomical construction of the stem of *S. pilifera* and *S. lepidophylla* differ but slightly, the leaves of the latter possess more elongated cells in the mesophyll. In *S. Pringlei*, the cells of the hypodermis and cortex also are similar (Fig. XI, 1) to those of *S. pilifera*, but there are 5 to 7 rows of cells in *S. pilifera* and *S. lepidophylla* from 7 to 9. Other species, e.g., *S. involvens*, *S. longispicata*, and *S. convoluta* possess the same characteristics as *S. pilifera*. There is, however, one striking difference in *S. imbricata*; specimens of which from Arabia, Zambesia and Abyssinia were examined. Individuals do not form flat, dense rosettes, like the other species of this group; the stems are more or less erect; the lower part is not branched but only covered with a few scale-like leaves (Fig. XI, 5). The upper half of the stem is branched as in other species. The various tissues are here similar to *S. pilifera*. The almost leafless and thick stem, is very hard and the cells are extremely thick-walled; the cells of the epidermis are smaller than those of the hypodermis. There is no difference in size between the cells of the hypodermis and most cell layers of the outer cortex; toward the centre the inner cortex becomes thin-walled (Fig. XI, 4). All the cells contain a large amount of oil; especially those of the thin-walled cortex. The cell walls of both sides of the lower stem are of the same thickness (Fig. XI, 2, 3) in all tissues. In the upper half of the stem, which is much branched and covered with both kinds of leaves, there is a marked difference in thickness in cell walls (fig. XI, 6, 7) between the upper and lower surfaces of each branch, as has been described in *S. pilifera* and *S. lepidophylla*.

Comparing the xerophytic Selaginellas of Group II and III with the hygrophytic species, it is apparent that the same tissues are present in all plants, although in modified form, corresponding with their particular environments. Xerophytic species adapt themselves easily to very moist and shaded environment; on the other hand, hygrophytic species are unable to grow in semi-arid situations.

A striking difference between plants of two different environments is that all the elements of xylem are much wider in hygrophytic than in xerophytic plants, and this feature stands in close relation to the water supply of the plants; moreover xerophytic species which have grown in a moist atmosphere have a more pronounced proto- and metaxylem. The cells of the cortex

are all large and thin-walled in the hygrophytic forms, and thick-walled and small in the xerophytic ones, as can be seen in comparing *S. pilifera* (Fig. VII) and *S. Galeottei*, a hygrophyte (Fig. XII). The hypodermal cells of the latter are, however, thicker walled, than the cortex, but do not contain any suberin or only to a slight extent. The cuticle contains suberin. The difference in width of the xylem vessels and cortex cells is given below.

Width in μ of vessels of xylem and of cortical cells in Selaginellas.

Name	Environment	Width of vessels of xylem	Width of largest cortex cells
HYGROPHYTIC PLANTS.			
S. Galeottei	moist greenhouse	40–70	80
XEROPHYTIC PLANTS.			
S. pilifera	from desert	10–20	50
S. pilifera	from moist greenhouse	20–30	62
S. lepidophylla	from desert	10–20	52
S. cuspidata	from desert	10–20	50
S. Pringlei	from desert	15–30	55
S. sanguinolenta	from exposed rocks	8–10	30
S. rupestris	from exposed rocks	20–35	40
S. rupestris	from greenhouse	25–42	45
S. arenicola	from sand barrens	20–30	40
S. densa	from exposed rocks	18–30	35
S. rupincola	from exposed rocks	20–30	40

The occurrence and number of stomata, which regulate to a considerable extent the transpiration of plants and the movement of water, are worth consideration. These stomata are all protected by a thick cuticle, which in species of Group I has a special air chamber, followed by a narrow passage through which the entrance between the two guard cells is reached. The situation of the stomata on the leaves is peculiar to each of the three groups. The most occur as a rule toward the midrib of the aligular surface of the dorsal and ventral leaves, since most air-spaces of the spongy mesophyll are to be found in this neighbourhood. The few stomata which occur on the ligular surface of both leaves have an unimportant rôle. The author in the following table summarises the presence of stomata in the plants with which he worked.

The principal question which arises after having studied xerophytic Selaginellas is the problem of the immediate protection and behaviour of the protoplasm of plants in desert and other semi-arid situations during extreme drought. Examining cells of above plants one notices a considerable number of large oval and round drops which ooze out of the open cells, when sections are

Occurence of Stomata on Leaves of xerophytic Selaginellas.

Name	Ventral Leaf			Dorsal Leaf			Environment and Locality
	Ligular Surface	Aligular Surface	Margin	Ligular Surface	Aligular Surface	Margin	
GROUP I.							
S. rupestris	none	pres.	none	none	pres.	none	Exposed granite rocks, Georgia, U.S.A.
S. rupestris	,,	,,	,,	,,	,,	,,	Shady moist greenhouse, Kew Gardens
S. rupincola	,,	,,	,,	,,	,,	,,	Exposed rocky place, desert, Tucson, Arizona, U.S.A.
S. arenicola	,,	,,	,,	,,	,,	,,	Dry pine wood, Florida, U.S.A.
S. densa	,,	,,	,,	,,	,,	,,	Exposed rocky place, Montana, U.S.A.
S. capensis	,,	,,	,,	,,	,,	,,	Exposed place, Orange River Colony, S. Afr.
S. Mildei	,,	,,	,,	,,	,,	,,	On rocks, San Luis, Brazil.
GROUP II.							
S. borealis	few	pres.	none	few	pres.	none	Exposed rocks, Kamschatka.
S. saccharata	,,	,,	,,	,,	,,	,,	On bluffs, Guadalajara, Mex.
S. mongolica	,,	,,	,,	,,	,,	,,	On rocks, Hsai-Watai, China.
S. sanguinolenta	,,	,,	,,	,,	,,	,,	On rocks, Karrum Valley, Afghanistan.
S. Douglasii	,,	,,	,,	,,	,,	,,	On trees in forest, Oregon, U.S.A.
GROUP III.							
S. lepidophylla	few	pres.	none	few	pres.	none	Exposed rocks, Guadalajara, Mex.
S. pilifera	,,	,,	,,	,,	,,	,,	Exposed rocks, Sonora, Mex.
S. pilifera	,,	,,	,,	,,	,,	,,	Greenhouse, Kew Gardens.
S. convoluta	,,	,,	,,	,,	,,	,,	Rocky exposed place, Uraguay.
S. cuspidata	,,	,,	,,	,,	,,	,,	Lava fields, Tlalpan, Mex.
S. cuspidata	,,	,,	,,	,,	,,	,,	Greenhouse, Kew Gardens.
S. imbricata	,,	,,	,,	,,	,,	,,	Rocks, Mount Dijot, Arabia.
S. Pringlei	,,	,,	,,	,,	,,	,,	Exposed place, Santa Eulalia Mts., Mex.
S. involvens	,,	,,	,,	none	,,	,,	Exposed place, Amurland, Siberia.
S. longispicata	,,	,,	,,	few	,,	,,	Rocky place, Porfiric Valley, Mex.

cut for microscopic examination. Alcanna readily stains these drops red, which is evidence of the presence of oil. This oil is to be found in very small drops in the protoplasm when examined in water; when the cell loses water or, during plasmolysis, the protoplasm shrinks, these drops get larger through union of several small ones. In what form oil is present when the cell has lost all its available water could not be observed, but the writer suggests that a film of oil forms around the entire protoplast or at least its vital parts, which is then able to enter the dormant state during drought; this condition is very likely the same as that of matured seeds, and especially those of Cruciferous plants. Neither

hygrophytic species nor xerophytic plants grown in a moist environment produce oil; the main product of C,H, and O is starch which is, however, less present in xerophytic plants grown in exposed places. This suggests that oil is a protection as well as a reserve food. Dead cells, like those of certain parts of the thick-walled cortex and especially of the hypodermis possess very large drops of oil, which frequently occupy the entire width of the cell.

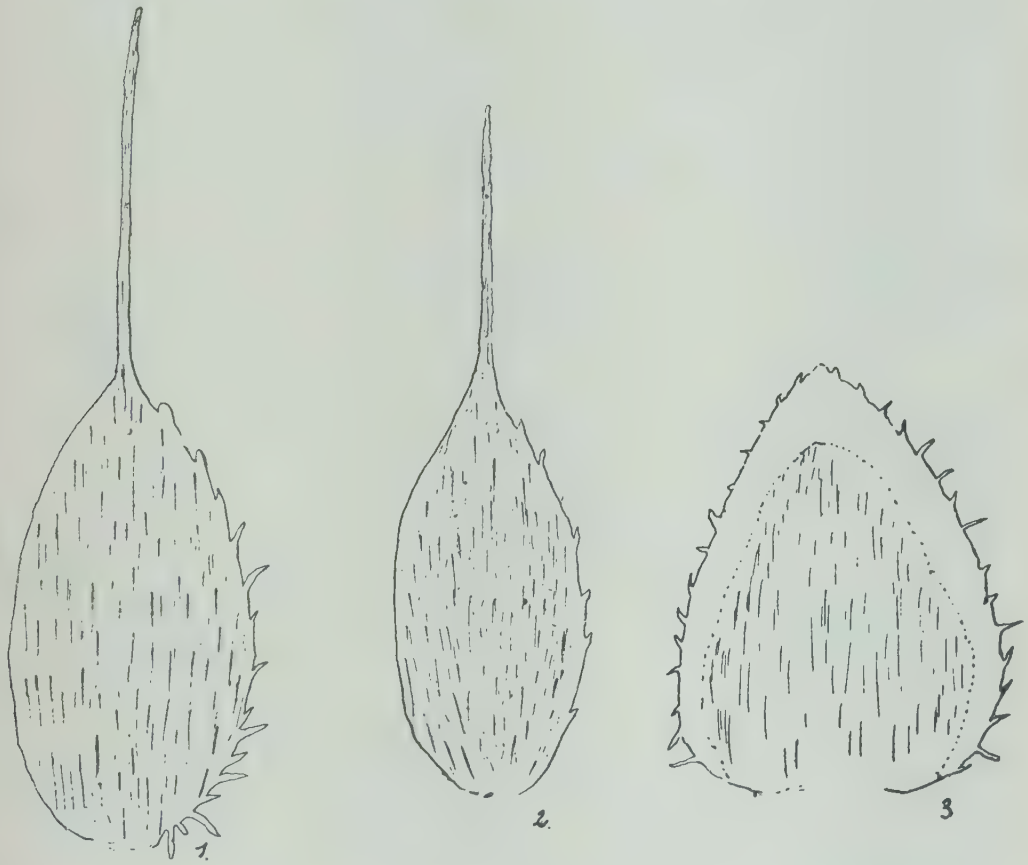

FIG. X. *Selaginella Pringlei*, 1, ventral leaf; 2, dorsal leaf. *Selaginella lepidophylla*, 3, ventral leaf.

The writer's study of the behaviour of xerophytic Selaginellas leaves many questions unanswered, among which the structure and action of the roots and rhizophores is of first importance, as is also a comparative study of osmotic pressure in cells of plants grown in the desert and in a moist atmosphere; further the development of the gametophyte and a closer study of photosynthesis have to be considered. Satisfactory results can only be obtained when plants are studied in their natural environment.

SUMMARY.

About six per cent of the known species of *Selaginella* are xerophytic. Their geographical distribution is closely associated with that of xerophytic ferns.

Comparing various species of xerophytic and hygrophytic Selaginellas one notices the very close proximity of the dorsal and ventral leaves in the former and the great distance between the succeeding leaves in most species of the latter. There is a striking similarity in the size of the leaves of all xerophytic species, while in all hygrophytic Selaginellas there is a great difference in the size of dorsal and ventral leaves. This similarity in size of leaves of xerophytic forms is of much importance from the photosynthetic standpoint; the ventral leaves produced under the influence of this

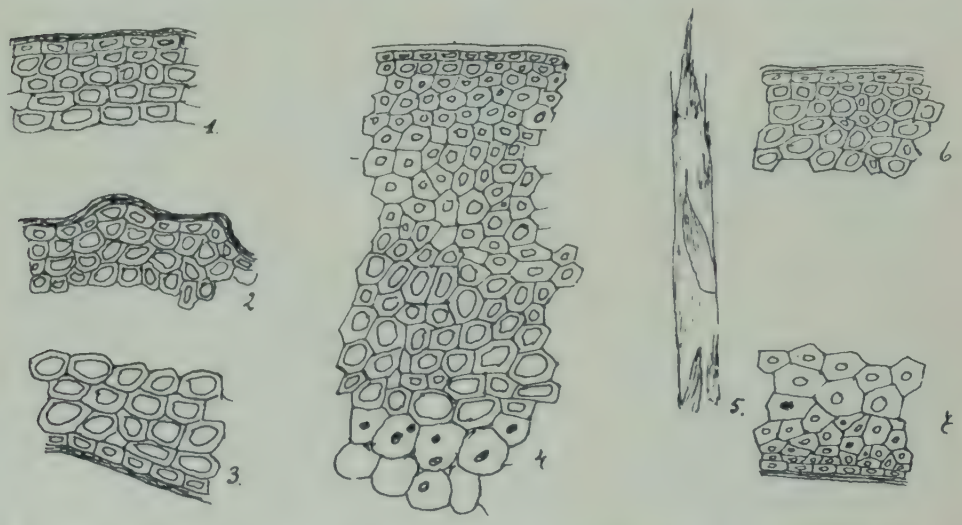

FIG. XI. *Selaginella Pringlei*, 1, epidermis and hypodermis. *S. imbricata*, 2 and 3, opposite sides of lower part of the stem, showing epidermis and hypodermis, both have cells with thin walls; 4, section of middle portion of stem; 5, part of lower half of the stem; 6 uppermost, and 7, lower surface of the stem above the middle. Note difference in thickness of cell walls of the uppermost part and lower part of the stem.

extreme environment contain but few chloroplasts, and most of the production of organic matter has to take place in the comparatively large dorsal leaves.

There are three groups of xerophytic Selaginellas. (1) Plants with vertical leaves, of the same shape and size. The apex of each leaf ends in a long awn containing no chloroplasts. The anatomical construction is sclerotic. (2) Plants having slender, wiry trailing stems, spreading over the ground or hanging from rocks and sometimes trees. (3) Plants having a spreading habit, stems often forming a flat, dense and close rosette, rolling into a cluster-ball during drought.

In the first group, the leaves, which stand in a vertical direction and are parallel with the stem, form a protection against the intense sun's rays. The growing points of the stems receive the rays directly, but the bundle of awns situated on the apex of the

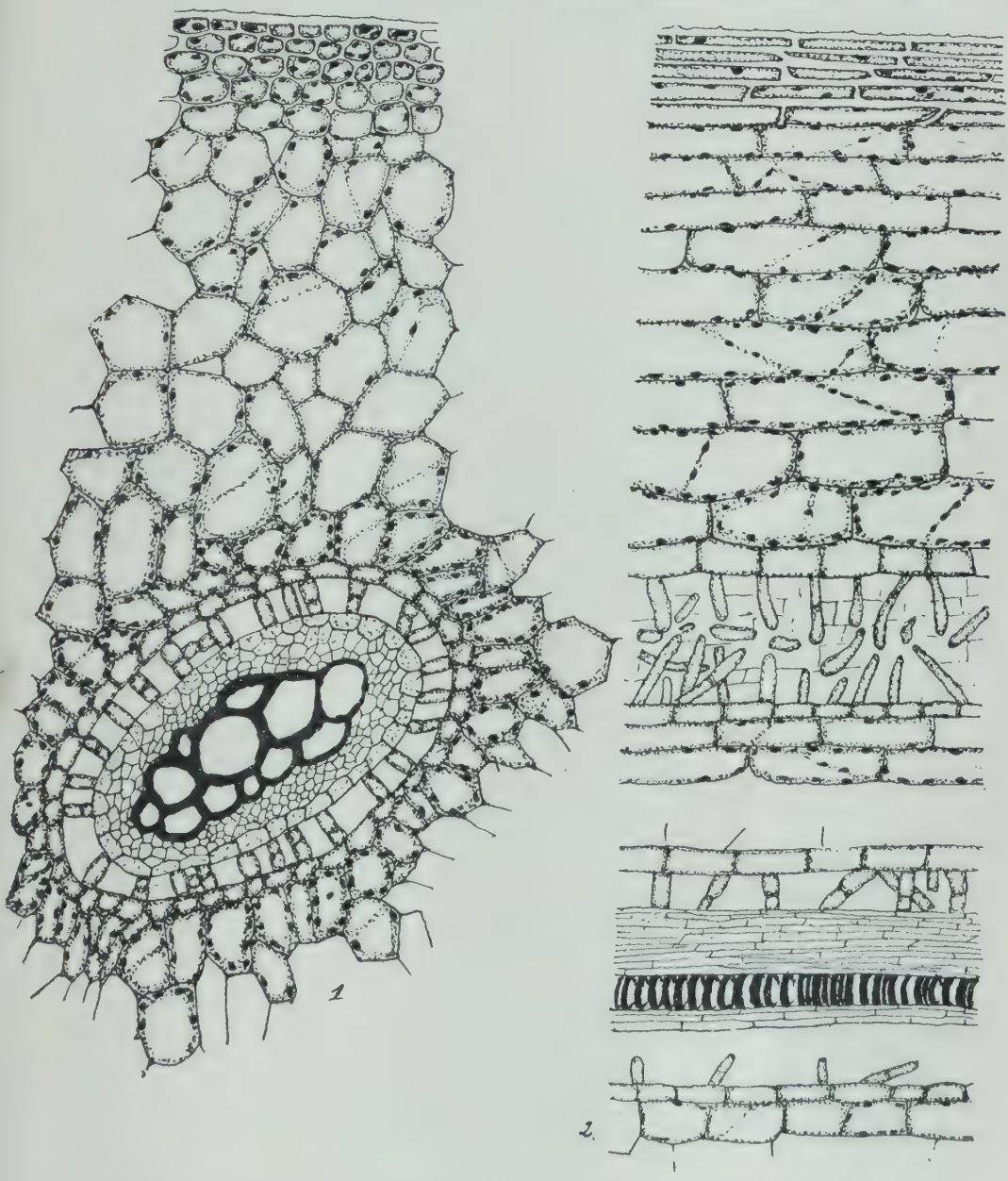

FIG. XII. *Selaginella galeottei*, a hygrophytic species from shady and moist greenhouse. Note large and thin-walled cells of hypodermis and cortex, and well developed xylem in comparison with *S. pilifera*, 1, cross section ; 2, longitudinal section.

leaves reflect the light entirely. All plants have a thick-walled epidermis, hypodermis and outer cortex, which are heavily impregnated with suberin. The leaves are all surrounded by

a thick-walled epidermis; the wings contain a well developed sclerotic tissue, all heavily suberized. The elements of the proto- and metaxylem are considerably narrower than those of hygrophytic species. Plants which were grown in a moist shady greenhouse develop horizontal leaves; the various tissues are neither as thick-walled nor as heavily suberized; the xylem has wider vessels. Some species are petrophilous, other are decidedly psammophilous.

The second group is composed of plants with a spreading habit; some show affinities with the last group, since they are able to roll up during drought. The anatomical construction is not as sclerotic as in the previous group, although the walls of the epidermis, hypodermis and outer cortex are very thick-walled. Some species produce a red pigment which is deposited in the cell walls of very exposed stems. In some forms the vessels of the xylem are very narrow, which is correlated with the low water supply and the very small leaves of the plant. The cuticle and other walls of the epidermis of the leaves are extremely thick. The mesophyll is well developed and possesses large air-spaces in the spongy parenchyma.

Plants of the last group are exceedingly well fitted for a semi-arid environment. The stems are densely tufted and curl up into a more or less close cluster; the leaves are placed horizontally on both sides of the stem.

During intense heat the exposed parts of the stem and leaves reflect the light considerably; these parts are white or brown to red-brown, according to their exposure to the heat. The brown color is always in the cell walls. On very exposed places the underside of some species is protected by a colloidal layer against extreme transpiration, and this retains the water for a long time when moistened.

The anatomical construction of all species shows a rather thin-walled hypodermis and cortex on the upper (inner) surface of the stem, and a thick-walled hypodermis and cortex on the lower (outer) surface. During drought the thin-walled tissue loses more water than the thick-walled tissue, which causes the plant to curl up; it absorbs more water when moistened which causes the plant to spread out. The statements of Leclerc du Sablon and Wojinorvić are misconceptions. These investigators state that the thick-walled tissues are on the upper side of the stem and absorb more water than the thin-walled tissues when moistened, and lose more water when drying. The hygrochastic movements are mechanical and can be also observed on dead plants. The plants increase in

weight after complete absorption of water from 42 to 54 per cent.

Xerophytic Selaginellas contain in their cells a considerable amount of oil; it is to be found in small drops in the protoplasm; when the cell loses water and the protoplasm shrinks, the drops unite and become larger, which suggests that a film of oil forms around the entire protoplast during drought, when it is able to enter its dormant state. Hygrophytic species do not produce oil, but starch, and this suggests that oil is also a reserve food for the xerophytic species, which produce less starch.

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MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER IV.

Non-Disjunction in Drosophila.

ANALOGOUS to the irregular distribution of meiotic chromosomes, which gives rise to such mutants as *Œnothera lata* and *Œ. scintillans*, is the phenomenon in *Drosophila* which Bridges (1916) has called non-disjunction. To make this matter clear it must be remembered that *Drosophila melanogaster* has four pairs of chromosomes of different sizes, including a pair of sex chromosomes XX in the female and an unequal pair XY in the male. These pairs separate like the others in meiosis, so that half the sperms have an X chromosome and half a Y, while all the eggs after maturation have an X. Furthermore, we need to know that the Y chromosome, as in other insects, is inactive, carrying no known factors and taking no active part in sex-determination. A large number of sex-linked characters are now known, including many eye colours, and as these characters are distributed in crosses exactly as the X chromosomes are distributed—each daughter receiving one X from her father and one from her mother while each son receives his single X from his mother—we must suppose that sex-linked characters are determined by the presence of the X chromosome and that, in short, the determiners for such character-differences are borne by the X chromosomes. Moreover, the phenomena of "crossing over" or separation of two sex-linked characters which went into the cross from the same parent, *i.e.*, carried by the same X chromosome, determine the relative position of such determiners in the chromosome, on the assumption that the farther apart they are along its length the more frequently crossing over (from the wrapping of the chromosomes around each other and subsequently breaking apart in new positions) will take place. On the basis of the percentages of crossing over, chromosome maps have been constructed for all four chromosomes, in which are indicated the relative positions of the various genes or determiners along their length. It will be understood that crossing over occurs between the members of a pair of chromosomes, but not between one pair and another. The amount of breeding work involved in thus determining that all the mutations fall into four linkage groups and the relative positions of the members of each group with reference

to each other, has been prodigious and is an achievement in itself. The data for sex-linked characters alone involved the breeding of over half a million flies.

Chromosome No. 1, the X, (see Morgan *et al.* 1915), contains all sex-linked mutations, since this is the sex chromosome. Such factors already number over 50, including a series of eye colours, bar eye with a reduction in the number of facets, yellow and sable body colours, forked bristles, club, miniature and rudimentary wings, and several lethal factors which prevent development when present in the homozygous condition. Chromosome No. 2 is the longest pair and contains such mutation factors as purple eye, curved and vestigial wings, and black body. No. 3, the next longest, as shown by linkage percentages, contains such eye colours as pink and peach, rough eye due to a peculiarity of the facets, ebony, sooty and sepia body colours, and beaded wings. The fourth group of factors, more recently discovered, and transmitted independently of the others in the Mendelian sense, contains only two known factors, bent wings and the eyeless condition. It evidently corresponds with the fourth, very small, pair of chromosomes.

It has long been known that crossing over, which may occur between the various members of each group, is confined to the female. The amount of crossing over is also independent of the way in which the factors enter an individual in a cross. Thus if they enter from the same parent (*i.e.*, in the same chromosome) any two factors tend to cross over with a certain frequency, while if they enter from different parents they tend with equal frequency to cross over so that both will be in the same chromosome in the offspring. In the male of *Drosophila* there is no crossing over between the X and Y or between any other pairs of chromosomes.

The probable reason for this has only recently been discovered (see Doncaster 1920, p. 235) by Metz. It apparently depends upon the fact that while in the egg there is a stage during maturation when the long, thin chromosomes are twisted round each other, there is no such stage in the male during the period preceding the separation of the chromosome pairs, the chromosomes remaining in a fairly condensed state during the whole growth period of these nuclei. Once again cytology furnishes the basis for the peculiarities in the phenomena of inheritance observed. In some other organisms (moths and fowls) crossing over takes place only in the male and not in the female, while in *Primula*, grasshoppers and rats it takes place in both sexes. That crossing over involves a break n the chromosome at a definite point, and not an indiscriminate

exchange of genes between a pair of chromosomes, is shown by the fact that when a number of factors are involved whose position at intervals along the chromosome is known from the crossing over percentages, a group of them go over *en bloc* and the rest remain in the chromosome (*i.e.*, group) where they were before. Thus (Morgan *et al.* 1915, p. 66) if a hybrid female is made up, having received from her mother the mutant factors yellow, white, abnormal, bifid, vermilion, miniature, sable, rudimentary, and forked, and from her father the normal allelomorphs of these together with the dominant mutant factor for bar eye, her formula may be written as follows: $\frac{y\ w\ a\ b_i \quad v\ m\ s \quad r\ f\ b'}{YWAB_i \quad VMS \quad RFB'}$ these factors all being present in the two X chromosomes. When such females were bred, they were found to produce the following kinds of eggs, with the frequency indicated:

Non-crossover eggs.

y w a b_i v m s r f b′ — 6
YWAB$_i$ VMS RFB′ — 8

Single-crossover eggs.

YWa b_i v m s r f b′ — 2
YWAB$_i$ v m s r f b′ — 2
y w a b_i VMS RFB′ — 2
YWAB$_i$ Vm s r f b′ — 1
YWAB^i VMS r f b′ — 1
y w a b_i v m s RFB′ — 1

Double-crossover eggs.

y w a b_i VMS RFb′ — 1

But such types as yWaB$_i$ VmS rfB′ were not found, showing that indiscriminate reassortment of the factors between a pair of chromosomes does not occur.

Double crossing over, in which the ends of a pair of chromosomes exchange while the central portion remains as before, lessens the effect of single crossovers and so is called interference. The result is as though the percentage of crossing over between certain points was reduced.

Now if a female with vermilion eyes is crossed with a wild red-eyed male, the vermilion being recessive the daughters will have red eyes like their father because they received his X chromosome with the red factor which is dominant to vermilion. But the sons will have vermilion eyes like their mother, since they received her X chromosome and only the inactive Y from the father. This criss-cross inheritance will always happen when the

father bears a dominant sex-linked character. About 50 such sex-linked mutations are now known in *Drosophila*.

But occasional exceptions occur, in which a female produces a daughter like herself or a son like the father. These primary exceptions by an ordinary XX female were found to be the result of an egg in maturation either retaining both X chromosomes or allowing both to pass out into the polar body. Such an egg will be XX or zero as regards its sex chromosomes. If such eggs are fertilized by ordinary sperm from a red-eyed male, the result will be as

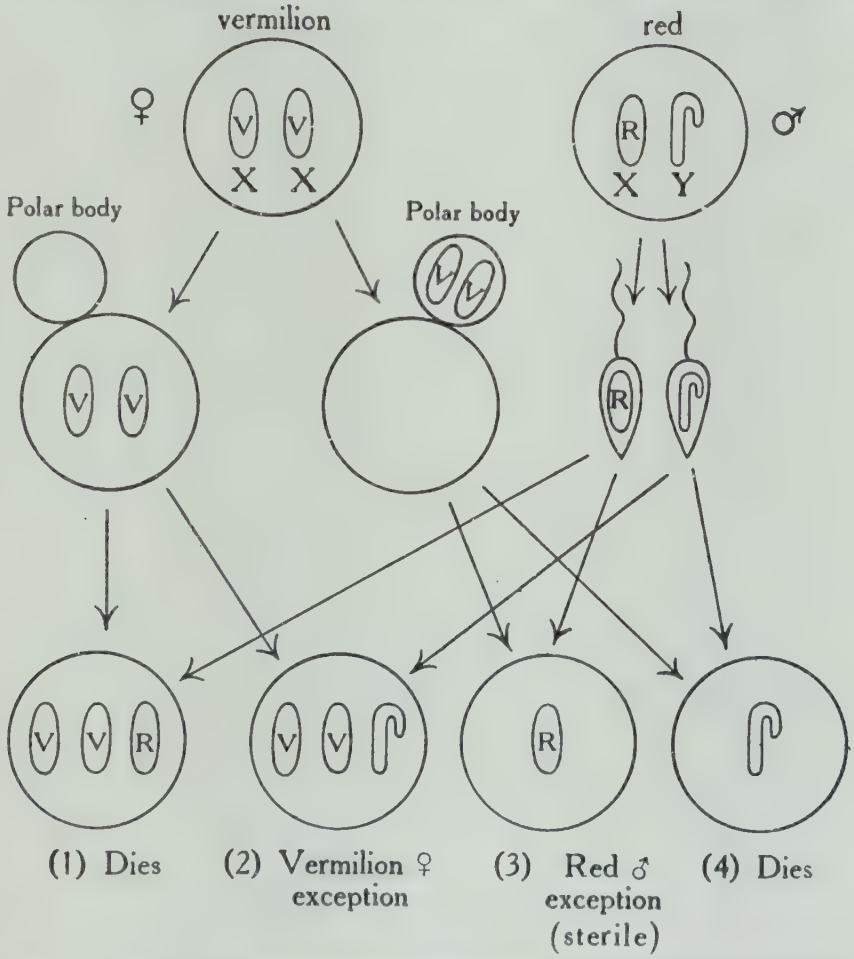
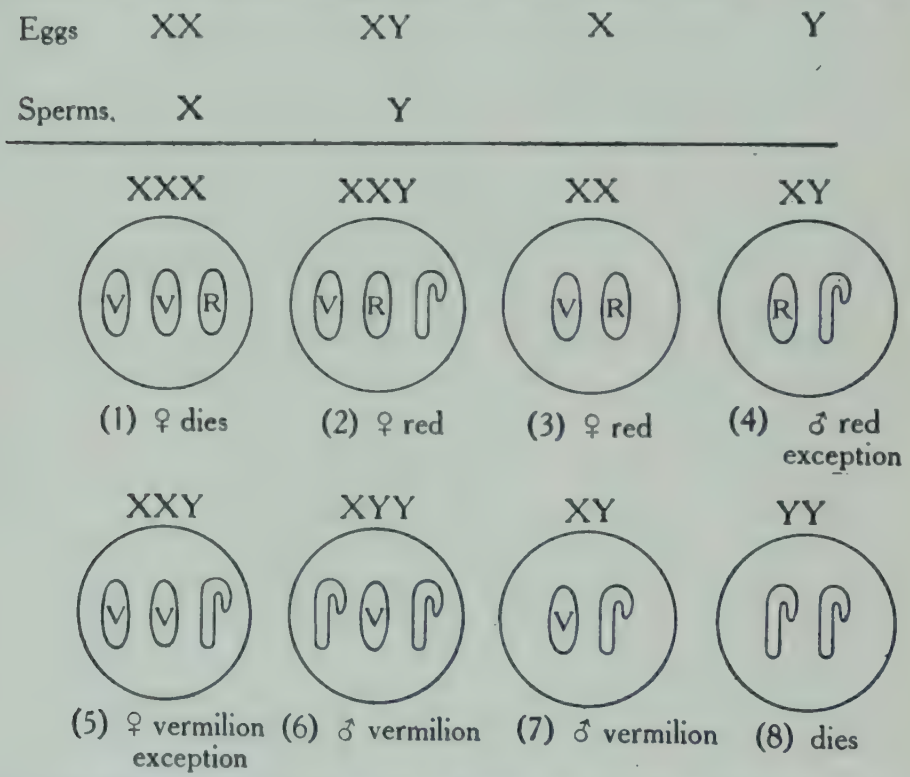


Fig. 1. Diagram of primary non-disjunction. Modified after Bridges.

shown in the diagram (Fig. 1). Four new types will result: (1) The XX egg + X sperm = XXX females which die. (2) The XX egg + Y sperm = XXY female having vermilion eyes and hence an exception to the criss-cross rule. (3) The O egg + X sperm = XO male which is sterile. It has red-eyes and is a patroclinous exception to the criss-cross rule. (4) The O egg + Y sperm = OY zygote which is not viable. Hence only

half of the primary exceptions survive. The XXY females are fertile and can be used for further breeding.

Non-disjunction also occurs in the male, giving XY and O sperm. The XY sperm would produce XXY daughters, like the XXY females above but with red eyes. They are therefore not exceptions, but will give exceptions in their offspring. Wilson (1909) observed three spermatocytes of Metapodius, another insect, in which X and Y went to the same pole in the reduction division. The XXY females give about 4% of secondary exceptions (*i.e.*, 4% of daughters like the mother and 4% of sons like the father) when crossed with a male having other sex-linked characters. This was



at first supposed to be due to a *factor* for non-disjunction. The exceptions were afterwards found to be due to the presence of the Y. After further breeding experiments it was predicted that cytological examination of the daughters of an exceptional female would show the presence of an extra chromosome in half the daughters while the other half would be normal. This prediction was completely verified.

Let us consider now what will happen in XXY females. Synapsis may take place between the two X chromosomes, leaving the Y unmated (homosynapsis), or it may be of the XY type (heterosynapsis). About 84% of the cases were formed by breeding

to be homosynaptic. After heterosynapsis the reductions will be XX—Y or X—XY. From the former the eggs after maturation will be ½XX and ½Y; from the latter, ½X and XY. Also from homosynapsis, the reductions will be X—XY or XY—X, since the unmated Y may remain in the egg or enter a polar body, and the eggs will therefore be ½X and ½XY. Hence 4 classes of eggs result: XX and Y 4% each, of single origin; X and XY 46% each, of composite origin. Therefore if such an XXY female having vermilion eyes is crossed by a wild male (red eyes), there will be 8 classes of zygotes, as shown in the diagram (Fig. 2).

Of these eight classes, (2) are not exceptions but would produce exceptions in the next generation, (4) are produced by the reverse of the ordinary method, *i.e.*, by the union of a Y egg and an X sperm. While themselves exceptions, they are ordinary males and can neither produce exceptions nor transmit the power of doing so, (6) are not exceptions, but some of their daughters will get the extra Y (from XY sperm + X egg) and so produce secondary exceptions. It was found that homosynapsis occurs much oftener than heterosynapsis, but otherwise the chromosome distribution is according to chance. That matroclinous exceptions had developed from fertilised eggs was shown by the presence of paternal characters derived from other chromosomes.

In XYY males, synapsis may be of the XY or YY types. If these are simply by chance there should obviously be twice as many XY as YY synapses. The synapsed chromosomes disjoin and the other one apparently goes equally to either pole. Hence in XYY males 4 classes of sperm will be produced, X and YY from heterosynapsis (small classes) and XY and Y from homosynapsis (twice as large and from two sources). These four classes of sperm fertilizing an ordinary female would give the following results:

Sperm	X	YY	XY	Y
Eggs	X			
	XX	XYY	XXY	XY
	♀	♂	♀	♂

Half the daughters will therefore be XX and half XXY, while half the sons will be XY and half XYY, again producing exceptions. Primary non-disjunction in the female, or failure of the sex chromosomes to separate in the egg, occurred 12 times in breeding experiments involving 20484 flies, or 1 in 1700. The fact that XO males are sterile shows that the Y chromosome has some function in spermatogenesis, if only to serve as a balance wheel.

In the cytological examination one female was found with 10 chromosomes, *i.e.*, XXYY. She was from a stock culture in which half the females should be XXY and about half the males XYY. Nearly half the eggs of such females are XY, and one-third of the sperm of an XYY male are XY. Hence XXYY females should frequently occur in this stock.

The relations of non-disjunction to crossing over are still more intricate and surprising in their results. In XXY females, in cases in which the synapsis was XY (heterosynapsis) since the X chromosome was in synapsis with Y, there could be no crossing over with X. The XX eggs should therefore always be non-crossovers, and this was shown to be true. Linkage experiments show that there is about 33% of crossing over between eosin and vermilion, *i.e.*, if they entered the cross in separate X chromosomes one-third of the eggs would carry neither factor or both in their single X. But when an XXY female carried eosin in one of her X chromosomes and vermilion in the other, the exceptional daughters were always like their mother in that they still carried eosin in one X and vermilion in the other. On the other hand, in the XY and X eggs from an XXY female, crossing over took place in the ordinary way.

Such XXY females have been obtained from three sources, (1) XX egg + Y sperm, (2) XY egg + X sperm, (3) X egg + XY sperm. In all cases the frequency of secondary exceptions is the same, which means that the method of synapsis is the same whether the two chromosomes came from the same or from different parents.

One must agree with Bridges that these results, which are only summarized here, furnish a definite proof of the chromosome theory of heredity. Exceptions which seemed at first to be unconformable to any possible chromosome theory of heredity have turned out to be a brilliant confirmation of the whole position. In no other case have breeding and cytological work been combined with more convincing results. The correctness of the point of view involved has been independently demonstrated, first by breeding experiments and then by cytological observation.

There are certain interesting and significant differences between the results of duplication of a chromosome in plants and animals. As we have seen, individuals containing an extra Y chromosome in the nuclei, or even an extra X as well (XXYY), show no external peculiarity and are only distinguishable by the

differences they show in hereditary behaviour owing to the different factors they carry, or by actually counting their chromosomes. The same is true of Metapodius (Wilson, 1909), in which some individuals were found having as many as six supernumerary chromosomes owing to irregular distributions of the Y chromosome in the reduction division, yet they were apparently indistinguishable from others with the normal equipment of chromosomes. This is in contrast to the conditions in plants, where, as shown in Chapter III, the extra chromosome is constantly associated with new external characters. Whether this is a general difference between plants and animals is unknown, but it may result from the fact that the cell unit in plants is a more rigid thing and less subject to regulation (in the physiological sense) from the structural point of view.

In *Drosophila* then, the detection of the presence of an extra chromosome is only by means of the factors transmitted, or by direct observation of the chromosomes. In *Œnothera* there is also a difference in the hereditary behaviour, nearly all the 15-chromosome forms splitting at least into the two parental types. But in addition the external characters are directly affected. Although the breeding results with plants are necessarily much slower, yet it is hoped that the nature of the chromosomal differences between the various 15-chromosome types will ultimately be determined.

It has been necessary to dwell upon these results in *Drosophila* at some length, for although an animal it is obvious that the results concerning linkage, crossing over, lethal factors and the conceptions of the linear arrangement of factors in the chromosomes will fundamentally affect our conceptions regarding the basis of heredity and the constitution of the germplasm in plants as well. Indeed, this has already been the case. Once it is generally recognized that in the morphology and constitution of the chromatin lies the chief basis for the inheritance of differences, then we shall be on safe ground for future experimental progress.

CHAPTER V.

Parallel Mutations.

For many years *Œ. lamarckiana* was the only Œnothera known to exhibit mutations. Then mutations were discovered in a race of *Œ. biennis*, one of which showed all the peculiarities of *lata*, but had the small flowers and other specific features of *biennis*. From this form the conception of parallel mutations and the recognition of their significance originated (see Gates, 1912a). Shortly afterwards Stomps (1912a) described independently the mutants *nanella* and *semigigas* from hybrids between *Œ. biennis* and *Œ. biennis leptomeres* Bartl. (=*Œ. biennis cruciata* de V.) but apparently without recognizing the significance of their parallelism to forms derived from *lamarckiana*. *Œ. biennis* mut. *lata* was later[1] described in detail and shown to have 15 chromosomes. It was clear that the same kind of germinal change was involved in both species. Two other probable mutations in *Œ. biennis*, one a red-nerved form parallel to *rubrinervis* Gates, the other resembling *lævifolia*, were also obtained. On these results the conception of parallel mutations was founded, and it has since been generally adopted by mutationists (see Stomps 1914, de Vries 1915b).

Equally striking mutations have now been obtained from several species of Œnothera, including such wild species as *Œ. grandiflora*, *Œ. stenomeres* and *Œ. pratincola*. In the last two species, some of the mutations are parallel to those described in *Œ. lamarckiana* or *Œ. biennis*, others are entirely dissimilar. A number of cases of clearly parallel mutations are put together in Table II, but a great many cannot readily be arranged in a table, and these will be discussed separately. From the table it will appear that three species have produced *lata* mutations (with 15 chromosomes), while five have produced mut. *gigas* (28 chromosomes) or mut. *semigigas* (21), and the same five species have given rise to dwarfs. These mutations have also occurred in various crosses. Virescence has also appeared independently in three species of Œnothera.

Let us now consider the history of some of these mutations, especially in *Œ. biennis* Linn., *Œ. stenomeres* Bartl. and *Œ. pratincola* Bartl., all of which have small flowers, are self-pollinated and rarely undergo natural crossing. The writer (1912, 1914)

[1] Gates & Thomas 1914.

obtained mut. *lata* from *Œ. biennis*, also a red-nerved (*rubrinervis*) type and a *lævifolia*. Stomps (1912a), in the cross *Œ. biennis* × *Œ. biennis leptomeres* Bartl. (*leptomeres*=*Œ. biennis cruciata* de Vries) observed one dwarf mutant (*biennis nanella*) and one *semigigas* (with 21 chromosomes). The *biennis* parent was descended from a rosette collected by Stomps on the sand dunes near Wykaan-Zee in 1905, which gave a uniform race. The *biennis leptomeres* was derived from a plant originally collected in 1900 by Ernst de Vries near Santpoort, Holland, and from which a constant strain was obtained. In 1903, one dwarf (*Œ. biennis leptomeres nanella*) arose in about 600 of the tall cruciate variety. The original *leptomeres* plant, when found in 1900, was surrounded by a number of normal *biennis*, and evidently had arisen as a mutation.

TABLE II.

PARALLEL MUTATIONS IN ŒNOTHERA.

Species	*lata*	*gigas*	*semigigas*	Dwarfs			*cruciata*	*elliptica*	*lævifolia*	Virescence
				nanella	*semialta*	*debilis*				
Œ. lamarckiana Ser.	X	X	X	X			(X)[1]	X	(X)[1]	X
Œ. biennis Linn.	X		X	X			X		(X)[1]	X
Œ. grandiflora Sol.		X	X	X						
Œ. stenomeres Bartl.		X		X						
Œ. pratincola Bartl.		X								
Œ. Reynoldsii Bartl.		X?			X	X				
Œ. suaveolens Desf.	X									
Œ. multiflora Gates [2]										X
Œ. grandiflora × *biennis* [3] F_2 and F_3	X		X?	X				X?		

The significance of the various species and varieties with cruciate flowers will be considered later. The first experiments with pure *Œ. biennis* were undertaken by Stomps (1914). He collected a rosette of this species at Beverwyk, Holland, in 1905, from which he obtained a pure line. Among over 900 plants belonging to the third and fourth generations, Stomps found 6 mutants, 1 *nanella*, 1 *semigigas* and 4 *sulfurea*. The last differs from

[1] When enclosed in parentheses, the form is a presumptive mutation, but has not actually been obtained in a pedigree culture.

[2] For a description of this "species," probably of hybrid origin, see Gates, 1914b.

[3] Davis, 1913.

the type of *biennis* only in having pale yellow petals. It is found occasionally on the sand dunes and must have originated as a mutation.

The well-known uniformity and constancy of *Œ. biennis*, together with the apparent impossibility of crossing in the regions from which these plants were derived, greatly enhances the importance of the mutations obtained from them. This species, the only one with which Linnæus was at first acquainted, was originally brought from North America in 1614—the first evening primrose to be brought to Europe.[1] It was soon naturalized on the Dutch sand dunes, where it has retained its characters with remarkable uniformity for three centuries until the present time. Davis (1914) admits that no species in cultivation has greater claims to be regarded as a pure species, and at one time was willing to admit that if mutations were produced by it they would go far to prove the correctness of the mutation hypothesis that the production of new forms is not merely a phenomenon of hybridity. Indeed it would be difficult to find any species whose claims to "purity" or freedom from crossing are better authenticated. Not only is it self-pollinated, so that crossing would be a rare event at best, but for three centuries in these Dutch localities it has been more or less completely isolated from its American relatives. Even if its ancestors were crossed before they left America, 300 generations of self-fertilization would be more than ample to reduce it to a homozygous condition again,[2] unless a condition of balanced lethal factors maintained it in a heterozygous state.

But the Drosophila work shows (Muller, 1918)) that such a condition of balanced lethals is not the result of crossing, but of alterations which arise in the germ-plasm. Another fact against the hybridity theory is this. The mutant *sulfurea*, which has been shown to arise occasionally in cultures, is also "far from rare" on the Dutch dunes (de Vries, 1915b). Apparently it was first mentioned in 1687 by Hermannus in *Hort. Acad. Lugduno-Batavi*

[1] For the early history of some of these forms see *Mut. Factor*, p. 47.

[2] Without dealing with the mathematical formulæ for inbreeding involved (see East and Jones, 1919, p. 91), it may be pointed out that even if a large number of independent differences were involved in an original cross, the population from self-pollination would be practically all homozygous by the tenth generation. The population would then be expected to contain a number of different homozygous types. It might be anticipated that the weaker of such types would fail in the struggle for existence. But if we examine the facts, we find that *Œ. biennis* in Holland is remarkably uniform and has always been so, never showing any variations on the dunes except the *sulfurea* mutation, and *leptomeres* with cruciate petals. There is thus a complete absence of data on which to found a hypothesis of hybridity, while the evidence to the contrary is strong.

Cat. under the name *Lysimachia corniculata non papposa, Virginiana major, flore sulphurea.*[1] It must then have been appearing as a mutation in the original stock brought from America. Other wild American self-pollinated species recently brought into cultivation have been shown to be doing the same thing, *i.e.*, producing mutations with varying frequency. We must recognize that the germ-plasm of a species is a vast aggregation of units, among which complicated relationships arise which express themselves in throwing off at intervals new forms.

The frequency with which the mutations in *Œ. biennis* appear has been studied by de Vries (1915b). He grew 8500 plants from the pure line of Stomps, derived from a single wild plant from which they were descended in the third and fourth generation. They included 8 dwarfs (mut. *nanella*) or 0·1%, and dwarfs also occurred in later generations. The population of 8500 also contained 4 *semigigas*, or 0·05%,[2] and 27 *sulfurea*, or 0·3%. The latter appeared among the offspring of all seven parent plants. This gives a total of 39 mutations, or 0·45%. This is a lower percentage than in *Œ. Lamarckiana*, but much higher than in Drosophila. Cultures of *Œ. biennis sulfurea* from four of Stomps' mutants also gave two dwarfs among over 1000 plants which flowered. These give the race *Œ. biennis* mut. (1913) *sulfurea* mut. (1914) *nanella*. In this connection de Vries also obtained two other mutations from crosses. *Œ. lamarckiana* × *Œ. biennis nanella* yielded 55 plants, which had the characters of *lamarckiana* × *biennis*, except one *lata* mutant. Again, in the cross *Œ. biennis semigigas* × *Œ. biennis*, he obtained 19 plants, 1 dwarf mutant, 10 *biennis* with 14 chromosomes, and 8 of a new type (described elsewhere) with 15 chromosomes. The appearance of two uniform types in this cross is significant, for it shows that the meiotic processes were taking place so as to reduce the chromosome number in the gametes to 7 or 8. Moreover the fact that the 15-chromosome type was uniform indicates that the same chromosome must have been the extra one in every case.

This brings us to the meaning to be attached to the term parallel in connection with mutations. It is obvious that each mutation of a given type is parallel to every other of that type.

[1] See *Mutation Factor*, pp. 66, 158. The fact that the early writers, although they recognized *sulfurea*, found no other variations of *Œ. biennis*, shows that it was as uniform then as it is now.

[2] If mut. *gigas*, appeared only from the union of two diploid gametes, its frequency should then be about 1 : 4,000,000.

For example, each time *lata* appears as a mutation from *lamarckiana* the change involved must be the same. Again, in the sense in which the term originated, *Œ. biennsis lata*, *lamarckiana lata* and *suaveolens lata* are all parallel forms. Going farther afield the *cruciata* forms from *lamarckiana* and *biennis*, if independent in origin, are obviously parallel, but a number of wild species (shortly to be considered) which are unrelated to each other have cruciate flowers as a specific character. Some of these may have a common descent from a cruciate ancestor, others have almost certainly originated independently as parallel mutations. Nor is it certain that the change involved is always the same. The Drosophila work has shown that two mutations may be so closely alike as to be scarcely distinguishable, and yet have different relations in the germ-plasm.

The conception of parallelism is perhaps even more fertile when applied to the comparison of variations in different genera. A cruciate mutation has appeared in *Epilobium* and a similar variation probably occurs in other genera. Again, the phenomenon of doubling in flowers, to be considered later, shows that doubling may occur as parallel mutations in wild as well as cultivated species of many families. The same of course is true of white varieties, which almost any species of flowering plant may produce. Laciniation of leaves, maximum anthocyanin development, nanism, lack of chlorophyll (though such a condition may arise from various genetic causes), doubling, and a number of other characters may be looked upon as probably at any rate parallel mutations. Thus *Œ. rubricalyx* and the copper beech may be parallel in that they involve in their origin the same kind of germinal change. But this cannot be assumed with safety until it has been proved by breeding experiments with each. Thus some forms of flower-doubling are dominant and some recessive, and white varieties may originate in a number of ways. The same is true of gigantism. The *gigas* mutations from four species of Œnothera (Table II) show exactly the same peculiarities of stoutness, increase of cell size, 4-angled pollen grains and tetraploid chromosomes, so that the change is obviously the same in all cases. But in other genera gigantism may occur with or without tetraploidy. This whole subject will be considered further in connection with the variations of wild species of plants and animals.

The cruciate character.

Coming now to the *cruciata* type of mutation,[1] *Œ. biennis* var. *leptomeres* of the Holland sand dunes differs from the species in having narrow, linear petals, somewhat crumpled and more or less greenish yellow. This constant form Stomps (1913) regards as a case of incomplete sepalody, in which the petals have become imperfectly transformed into sepals. In *Epilobium* he describes a somewhat different form, *E. hirsutum cruciatum* de V., which originated from a group of a dozen plants (perhaps derived by stolons from one) and breeds true. The plants were found by Mr. John Rasor in Woolpit, Bury St. Edmunds, and seeds were sent to de Vries. They differ from the type in having, in place of the large, obcordate, lilac petals, small greenish scales shorter than the sepals, and pointed. That this is not a case of arrested development is shown by examining the young buds of the species. The petals are broad and obcordate even while still small and colourless. The buds of the cruciate form show also a tendency to dry up and fall when young. This appears to be a more complete case of sepalody. Crosses between type and variety gave a Mendelian ratio. Thus *E. hirsutum cruciatum* × *E. hirsutum* gave an F_2 of 323 plants, of which 245 were type and 78 variety. Also the reciprocal cross produced 177 plants in F_2, 130 of which were type and 46 variety, while one failed to flower. The sum of the two ratios is 375 : 124, showing that the *cruciata* mutation is a simple Mendelian recessive character.

Not only does the cruciate mutation from *Œ. biennis* differ from that of *E. hirsutum* externally, but also in its hereditary behaviour. For in reciprocal crosses of *Œ. biennis cruciata* with the parent type, while the F_1 is normal and the F_2 splits into the two original forms, yet the ratios are not Mendelian. Stomps unfortunately gives no figures, but states that whichever form is used as the male parent, that form appears in the greater number of the F_2 progeny. The cruciate forms in these two genera, while comparable in general, are not therefore strictly parallel forms.

Elsewhere (1913a, p. 25) the writer has shown that, whatever the origin of *Œ. lamarckiana* var. *cruciata*, both normal and cruciate flowers may occur on the same plant. This somatic

[1] See also *Mutation Factor*, p. 21. In addition to the specimen collected by Ernst de Vries, others have been found on the Lüneburg Heath, and they have been reported from other parts of Holland, probably from independent mutations.

segregation is apparently the same type of behaviour as was found[1] in the F_2 and F_3 of crosses between the large-flowered *Œ. rubricalyx* and the small-flowered *Œ. biennis*, in which large and small flowers frequently appeared on the same plant, and even long and short petals, of varying lengths, on the same flower. It is possible that this race of *Œ. lamarckiana* var. *cruciata*, which emanated from the Bremen Botanic Garden, may have originated by a cross between *Œ. biennis leptomeres* and *Œ. lamarckiana*. This hypothesis is supported by the short style in the flowers of this race, so short that, like *Œ. biennis*, nearly all the flowers were self-pollinated. But in crosses between *Œ. biennis* and its cruciate mutation there are no reports of this vegetative segregation, with both types of flowers on the same plant.

As a result especially of the studies of MacDougal (1905) and Bartlett (1914a), a number of cruciate species and varieties are now accurately known. As Bartlett points out, it is clear that these have not had a common origin, but they have arisen independently from different stocks, some more remotely and some more recently, just as var. *leptomeres* apparently originates even now from *Œ biennis* L. The first cruciate form to be discovered was *Œ. cruciata* Nutt. Its taxonomic history is given by Bartlett. Nuttall found it in Massachusetts and sent seeds of it to several botanists. Don grew it in 1824 and described it under Nuttall's name. The species which is still cultivated in botanical gardens under this name is quite likely descended from this original source. Its variable petals indicate that it has been crossed with a broad-petalled species, and it is now called *Œ. cruciata*, var. *varia*, de Vries.[2] In the sixth edition of Gray's Manual (1889) it was classed as probably a rare garden sport, since no specimens had been collected except in gardens, subsequent to the original collection over 60 years earlier. In later years cruciate specimens were collected in Vermont.

The interest awakened in wild North American Œnotheras by the work of de Vries, soon led to the discovery of other forms. Seeds of a cruciate form which had been collected at Sandy Hill, New York, near Lake George, in 1902, were divided, part of them being grown by MacDougal (1905) at New York, and a larger number by de Vries at Amsterdam. This material contained two

[1] See Gates, 1917a.

[2] De Vries found that this variety segregated roughly into three groups, (1) cruciate, (2) intermediate, (3) broad-petalled. The latter is constant except for rare cruciate bud mutations.

distinct types, one with rather broadly linear petals and rather thick flower-buds, the other with narrowly linear petals and slender flower-buds. A third cruciate type grown at Amsterdam in 1903, from seeds collected at Jaffrey, New Hampshire, differed in having a much longer calyx tube, and a more slender, less nutating stem. MacDougal (1905) gave descriptions of a third type from the Lake George seeds, which he identified with the New Hampshire form, but this identification is doubtful, as Bartlett points out. None of these three types is the same as *Œ. cruciata* Nutt. which came from Massachusetts. The two Lake George forms were described (Bartlett, 1914) as *Œ. atrovirens* Shull and Bartlett and *Œ. venosa* Shull and Bartlett. These may of course be cruciate varieties of the local species where they occur, but it seems more probable that they represent independent species. This would indicate that they have undergone further evolution since the cruciate mutation took place, or that the parent broad-petalled type has since become extinct.

Herbarium specimens with cruciate flowers, which have been placed under *Œ. cruciata* Nutt., but no doubt belong to several distinct types, have been recorded (Bartlett, 1914), from Nova Scotia (Sable Island), Maine, New Hampshire, Vermont, New York and Massachusetts. Another cruciate type with small flowers is represented by a specimen in the British Museum[1] collected in British Columbia in 1909—evidently an independent local variety or species. Bartlett also grew 50 plants from seeds of one individual collected at Springfield, Missouri. They were uniform with the exception of one plant, a single branch of which bore cruciate flowers. The petals were narrowly oblong, rather than linear. This suggests previous crossing with a cruciate mutant, which may very well have occurred in the field. Bartlett has cultivated a cruciate Œnothera from Mobile, Alabama, and describes another one, *Œ. stenomeres*, from Montgomery, Co. Maryland, which has given rise to mutations. Yet another cruciate species has been cultivated by Shull from Long Island, and has been described as *Œ. cleistantha* Shull and Bartl. (Bartlett, 1915e). It is not closely allied to any other known species, and the origin of the cruciate feature is therefore probably of ancient date. The flowers as a rule never open, and the most striking features of the species are its extreme leafiness and dense branching. It is obvious that the possibilities of natural crossing in this species are

[1] Gates, 1915a, p. 21.

very remote indeed. A minute but distinctive difference is in the large hairs of the calyx. On the bud-cone they are strongly ascending except around the top of the hypanthium where they are retrorse or perpendicular.

The cruciate form from Jaffrey, New Hampshire, is described by Bartlett, in the same paper, under the name *Œ. Robinsonii*. There is said to be "enough likeness between *Œ. venosa* and *Œ. Robinsonii*, so that a close relationship between them seems not unlikely." The differences from *venosa* are chiefly in the smaller size of *Robinsonii*, its more sharply dentate leaves, narrower bracts, longer more slender buds with dense erect viscid puberulence, and shorter calyx tips. The range of variation in bud length overlaps, however, and most of the differences are only obvious in the living plants. These two forms evidently represent closely allied elementary species rather than species in the Linnean sense. Both having cruciate flowers, one from New York State, and the other from New Hampshire, in the absence of local species of which they could be varieties the common character of cruciateness probably originated some time ago, and we may suppose that the series of small differences which distinguish the two species throughout have originated since.

Contrasted with these forms, in which the cruciate character appears to be of relatively ancient origin, is another cruciate species, *Œ. stenopetala* Bicknell, described from Nantucket Island in 1914. It is closely allied to the broad-petalled species *Œ. Oakesiana* Wats., from which it is probably descended. Yet the two have diverged in certain respects. In the case of *Œ. biennis leptomeres*, which apparently is still appearing as a mutation from *biennis* in Holland, the single difference in the flowers is unaccompanied by any other differences. This series is a most instructive one as a basis for contrasting the conspicuous unit difference of sudden and repeated origin, with the other smaller differences relating to all parts of the plant, by which the species have subsequently become differentiated. Whether the same type of evolutionary change is represented in both cases, is a matter worthy of close and prolonged study. By comparison and crossing of these cruciate forms, definite evidence might be obtained on this point. In many cases such elementary species differ from each other in physiological characters or methods of reaction to environment. An intensive study should make it possible to determine what relation if any these physiological and morphological differences bear to each other.

Cruciateness affords the most conspicuous and instructive examples of parallel mutations among wild Œnotheras. There are indications that the red hypanthium, which is the most conspicuous feature of the mutant *rubricalyx*, may also be paralleled, though in a less degree, by certain wild species. Thus *Œ. rubescens* Bartlett (1914b) has buds and hypanthia which are pale red. It would appear to agree in this feature with the form, probably hybrid in origin, which the writer[1] described from Lancashire under the name *Œ. rubrinervoides*. A small-flowered undescribed species, *Œ. columbiana*, from near Washington, is said by Bartlett to have "conspicuously red hypanthia." The writer has pointed out elsewhere[2] that the deep red of *rubricalyx* may become pale red by crossing and then back-crossing with a greenish-budded species. Thus in (*Œ. rubricalyx* × *grandiflora*) × *grandiflora*, if the female parent is heterozygous for the red factor, segregation into types with red or green hypanthia will take place, but the red will be much paler than in the selfed offspring of the female parent plant. In other words, the colour is diluted and the red remains permanently pale in the selfed offspring of such plants, deep red only being restored by a back-cross with *rubricalyx*. Red or reddish hypanthia in plants from all these different sources, indicate its appearance through independent variations in different species.

Parallel Mutations in Drosophila.

Various features of the Drosophila work will be discussed later. In *D. melanogaster* (*ampelophila*) certain mutations have occurred repeatedly. Thus (Morgan, 1919) white eyes have appeared independently three times, vermilion eyes at least six times, rudimentary wings five times, cut wing four times, truncate and notch wings each several times, but in the last two cases the change involved may not always have been the same.

In the last five years a number of mutations in six other species of Drosophila have been recorded. This includes a new eye-colour (scarlet) in *D. repleta* (Hyde, 1915a), another sex-linked mutation (light grey thorax) in the same species (Sturtevant, 1915), a wing mutation (jaunty C) in *D. confusa* (Hyde, 1915b), one in *D. tripunctata* (Metz and Metz, 1915), three mutations (extra bristles, triangle wing veins and short wing veins) in *D. obscura* Fall., and one (chocolate eye-colour) in *D. similis* Will. from Cuba (Metz, 1916b). In "species B," now known as *D. virilis* Stt., a more detailed study

[1] Gates, 1914b. [2] Gates, 1914a, 1915f.

of the mutations has been made. In four successive papers (Metz, 1916a, 1916b, 1918, 1920) a great many interesting facts have been recorded. *D. virilis* is known (Metz, 1914, 1916c, 1916d) to have six pairs of chromosomes, including one pair of small or m-chromosomes, whereas *D. melanogaster* has 4 pairs. In the latter species it has been shown that the 200 or more mutations all fall into the corresponding four groups. In *D. virilis* Metz (1920) has recently reported a total of 27 mutations, including 14 which are sex-linked (Group I), 3 in Group II, 4 in Group III, 3 in Group IV, and 3 in Group V. No mutations have yet been found corresponding to the small pair of chromosomes, but the late appearance of mutations from such small chromosomes is to be anticipated on the laws of chance, and the two known members of the corresponding group in *D. melanogaster* were not discovered until a very large number of mutations were known.

In an earlier paper (Metz, 1918) dealing with eight sex-linked characters in *D. virilis*, half of them were found to correspond closely to mutations of *D. melanogaster*. These four were yellow body-colour, magenta eye-colour, glazed eye-surface, and forked bristles on the thorax. The yellow mutation is slightly darker than in the case of *D. melanogaster*, but this is to be expected if the changes correspond, since the normal *virilis* is a darker species. In the forked mutation " the morphological correspondence is complete even to the smallest detail." Yellow and forked are not only sex-linked mutations, and hence in the X chromosomes, in both species, but their linkage relations are shown to be similar, so that they occupy corresponding positions in the X chromosome, yellow being terminal and forked about 55 units from it as measured by the percentage of crossing over. There are indications that the actual amount of crossing over is greater in *D. virilis*.

Confluent, referring to the veins on the wings, is another mutation which has its counterpart in *D. melanogaster*. It is a dominant, is not sex-linked, and when present in a homozygous condition has a lethal effect, as shown by the ratios of confluent in crosses and by the absence of homozygous individuals, though there is still a possibility that some may occur in *D. melanogaster*. Black body and morula-eye are other non-sex-linked mutations occurring in both species.

The six pairs of chromosomes in *D. virilis* have apparently been derived by transverse segmentation of two long boomerang-shaped pairs of chromosomes in *D. melanogaster*, the other two

pairs remaining unaltered. The evidence from those parallel mutations with similar linkage relationships shows that even the finer elements of the germ-plasm have maintained their relative positions and potentialities from species to species. This indicates a degree of static fixity combined with mutation in single elements which is truly remarkable, indicating that even the finer details of structure in the germ-plasm may maintain their spatial relationships for long periods. A number of the mutations in *D. virilis* have not appeared in *D. melanogaster*, though it does not follow that the latter species is incapable of producing them. At present it is quite unknown why one mutation rather than another appears at any given time, though the evidence is strong that each represents an actual transformation of a germinal element, and not merely a loss.

Clearly, the conception of parallel or homologous mutations is destined to be a very useful one in germinal analysis and in the study of relationships. In the next chapter we will consider its application to the study of variations in wild species.

LABORATORY NOTE.

NOTE ON AN IMPROVED METHOD FOR DEMONSTRATING THE ABSORPTION OF OXYGEN IN RESPIRATION.

I HAVE for some time been dissatisfied with the method which, I believe, is most generally employed in lectures and practical classes for demonstrating the fact that germinating seeds remove oxygen from the air by the process of respiration.

The apparatus, as figured in Darwin and Acton's "Physiology of Plants" (Fig. 15) or in Keeble's "Practical Plant Physiology," consists of a filtering flask fitted with a cork and containing germinating seeds and a test-tube with strong caustic potash solution to absorb the carbon dioxide produced. To the side tube of the filtering flask is attached a long vertical glass tube, the lower end of which dips into a dish containing mercury. The carbon dioxide produced by the respiring seeds is absorbed by the caustic potash, and that some oxygen is used up in the process is shown by the mercury rising in the vertical tube.

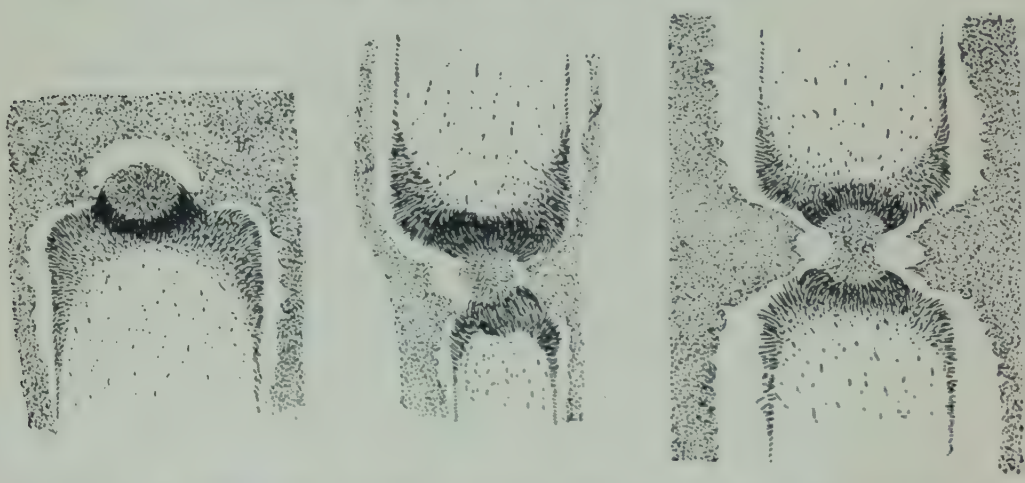
The objection to this form of apparatus is that the vertical column of mercury acts principally as a manometer registering a decrease in pressure, and the level of the mercury rises only a very few inches. So the fact that the germinating seeds are capable of using up in respiration all or nearly all of the oxygen in the flask, amounting approximately to one-fifth of the volume, is insufficiently demonstrated by the experiment.

I would suggest the slight modification in the apparatus shown in the accompanying figure, which, I think, requires but little explanation, as an improved method of performing the experiment. In practice it has been found to give good results.

The filtering flask containing some peas, which have been previously well soaked in water to start germination, rests on the table. The strong caustic potash solution is contained in a short wide specimen-tube, which is suspended by a loop of cotton from a bent pin stuck into the cork of the flask. The horizontal glass tube, connected with the side tube of the flask by a piece of indiarubber tubing, has its last inch or so bent at right angles, and dips into a dish nearly full of mercury supported on a wooden block.

The absorption of the oxygen by the germinating peas causes the mercury to be drawn into the tube, whence it runs into the flask and collects at the bottom, lifting up the seeds which float on its surface, thus showing clearly that a considerable amount of oxygen has been taken from the air contained in the flask during respiration.

The horizontal tube should slope very slightly upwards towards the flask to prevent any mercury running down into the flask by its own weight, and the level of the mercury in the dish should be kept only a little below the level of the side tube so that the mercury will require to be raised only a slight vertical distance.



If a graduated glass cylinder with a side tube could be substituted for the filtering flask, the apparatus might be employed for rough quantitative work. The objection to using an ordinary graduated glass cylinder and bending the proximal end of the mercury tube at a right angle so that it might pass through the cork closing the mouth of the cylinder, would be that the difference of level between the extremity of the tube inside the cylinder and the level of the mercury in the dish outside would cause this tube to act as a siphon when the mercury began to run into the cyliuder.

On the other hand, if one tried to avoid this happening by keeping the mercury in the dish at a slightly lower level than the opposite extremity of the tube, a negative pressure sufficient to affect seriously the result of a quantitive experiment would be required to raise the mercury in the tube.

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HYBRIDISM AND CLASSIFICATION IN THE GENUS ROSA.

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IT is generally recognised by students of the British Flora that the genus Rosa presents interminable difficulties in connection with the classification of its innumerable forms into anything like a satisfactory or natural system. This fact, it seems to me, is reflected in the ever-increasing number of names which go to swell an already lengthy British Rose List. Scarcely a year passes which does not witness the publication of new "species" or "varieties" which are considered by their authors as deserving distinctive names because the plants show a few differences, very often only minor ones, from allied species.

Among the earlier workers we find that Baker (1869) in his *Monograph of British Roses* is content with thirteen species (eleven, if we omit *R. rubella* Sm. and *R. pomifera* Herrm. which are doubtfully native) and a moderate number of varieties. On the other hand, the London Catalogue of British Plants (1908) enumerates twenty-five native species and a large number of varieties, many of the additional "species," of course, being Baker's varieties, while in the List of British Roses by Wolley-Dod (1911) about one hundred and seventy names appear. Since this author expresses no opinion as to the relative value of the names, it is difficult to say how many are intended to stand as species.

There are probably no plants more variable than roses and it is perhaps not too much to say that no two bushes of the same "species" are quite alike in all the technical characters relied upon by rhodologists for making a diagnosis. In the case of many micro-species it is found on investigation that authentic specimens collected or named by the authors themselves neither agree with the original

descriptions nor with one another. If the creation of new names continues at the present rate and according to the present system or want of system, the time will soon arrive when it will be impossible to say more of any member of the genus than that it is a rose. To make a determination and to give a binomial will become the work of a few specialists and there need be little hesitation in predicting that no two specialists will agree.

There is, no doubt, a strong tendency to place an ever finer construction on the idea of species whenever a genus is submitted to critical investigation and it is contended by many that the Jordanian practice of splitting the "Linnean species" into innumerable forms or micro-species has, in many instances, been carried to an extreme. Whatever the advantages or disadvantages of this practice may be, it brings us face to face with the problem of deciding what forms are to be regarded as worthy of specific rank. On this question, in so far as it concerns the genus Rosa, a unanimous opinion is not likely to be forthcoming, for "species" of Rosa must, in the present state of our knowledge, rest largely on differences which are in themselves artificial, and the chief difficulty is to decide what are really important and what are unimportant differences. It is gradually being realised that external morphology alone is inadequate for the solution of such problems, yet it is remarkable that still very few "critical species" among British plants have been subjected to the test of experimental investigation. Only by culture, combined as far as possible with cytological study, will it become possible, I think, to determine finally the genetic relationships of the numerous micro-species into which old, well-known species like *R. canina* Linn. have been split.

Regarding purely morphological investigation, it may be of interest to refer here to the work of Parmentier (1898), who endeavoured to throw some light on the problem by following the anatomical method. This worker, after an exhaustive enquiry into the detailed structure of the plants, divided the genus into primary species, morphological species, morphological sub-species and secondary forms. But this does not appear to have produced a better or more natural classification than that adopted by systematists. We find, for example, that while *R. canina* L. ranks as a primary species, *R. lutetiana* Lém., *R. dumetorum* Thuill. and *R. coriifolia* Fr. belong to the third category and *R. glauca* Vill. is a mere secondary form. Whatever the value to be attached to these forms of the aggregate *R. canina*, systematic students are

generally agreed in holding *R. glauca* Vill. to be as good a "species" as *R. lutetiana* or *R. dumetorum*. A knowledge of the anatomical construction of plants is useful and often very helpful, but taken alone it is not always sufficient to solve the problems of relationship.

One of the most striking results of the intensive study of British plants is the increasing number of hybrids that are being recognised. One need only mention such genera as Viola, Epilobium, Mentha and Salix. The presence of hybrids renders the classification of such genera extremely difficult, and it is not improbable that the difficulty in classifying roses may be largely due to hybridisation and segregation, complicated, it may be, by re-hybridisation. When one considers the general prevalence of wild roses, the frequent association of numerous species and forms in the same habitat, the large numbers of flowers produced by fully developed plants, it becomes evident that there must be abundant opportunities for natural crossing.

Several hybrids, in the sense of crosses between distinct species, have been recognised among British Roses. The commonest is *R. involuta* described by Smith, *Fl. Brit.* 1804, from material collected in the West of Scotland. It was not until 1884, however, that its hybrid origin was suggested, when Christ promulgated the idea that *R. involuta* Sm. is a natural cross between *R. pimpinellifolia* and *R. tomentosa*. This view is now universally accepted. *R. involuta*, though not common, is fairly widely distributed in the North of England and in Scotland, and it may be expected to occur wherever the two parents grow together. Numerous forms of the hybrid are to be found and many of these had received varietal names before the hybrid nature of this rose was realised. While *R. pimpinellifolia* shows little or no variation, *R. tomentosa* is decidedly a polymorphic species and considerable variation in *R. involuta* need not, therefore, be unexpected. In general, the characters of the hybrids are more or less intermediate between the unlike characters of the two parents, but some of the forms bear a greater resemblance to one or to the other parent, and it is not impossible that this may be due to *R. pimpinellifolia* being the seed-parent sometimes and *R. tomentosa* at other times. The hybrid plants are usually vigorous, flower freely and are more or less sterile, thus showing some of the attributes of hybrids between distinct species. Whether these hybrid forms of *R. involuta* breed true or whether they segregate is unknown, but the work of Brainerd (1906) on Viola suggests the need for similar investigation in the case of our natural rose hybrids.

Again, *R. hibernica*, described by Templeton in *Trans. Dublin Soc.* III. 1803, from plants found in the North of Ireland, is now regarded by all rhodologists as a hybrid between *R. pimpinellifolia* and *R. canina* Linn. sp. agg., although this view was not generally accepted when first advanced by Christ in 1875. *R. hibernica* is a comparatively rare plant, being known from only a few vice-counties in the North of England and from a few in Scotland, besides its two stations in Ireland, and apparently only the glabrous variety has been found on the Continent. The typical plant has leaflets hairy at least on the nerves below which is sufficient evidence to show that the second parent is a *dumetorum* or a *coriifolia* form, probably the former if the sepals become reflexed, the latter if the sepals become erect. *R. hibernica* var. *glabra* Baker has glabrous leaflets, and possibly in this case the second parent is a form of *R. canina* or of *R. glauca*, both of which are without pubescence on the leaves. *R. hibernica*, like *R. involuta*, is almost universally sterile and the remarks made in the discussion of the latter apply equally to this hybrid.

R. pimpinellifolia hybridises also with *R. rubiginosa*, but the hybrid is extremely rare. The British forms, the first of which was recognised as recently as 1896, have not received a binomial, but they are not markedly different from the French forms of the hybrid known as *R. biturigensis* Bor. The hybrid is most abundant on the coast of Haddington, where it grows in association with both parents. It is remarkably luxuriant, some of the bushes attaining a height of eight or nine feet. The plants are not so obviously sterile as the majority of *R. involuta* and *R. hibernica* forms, and two distinct types are recognisable in the shape of the fruit. In one the fruit is ovoid or oblong, recalling that of *R. rubiginosa*, in the other it is globose and therefore similar to that of *R. pimpinellifolia*.

A hybrid of *R. pimpinellifolia* and *R. mollis* has been recorded from several vice-counties in Scotland, the first record being based on the determination of specimens from Sutherland by Crépin. Similar plants have been discovered in Banffshire and in Perthshire and in all cases the evidence tends to point to *R. mollis* as the second parent. In addition the following hybrids, which do not involve *R. pimpinellifolia*, are recorded by Wolley-Dod (1911)—*R. arvensis* Huds. × *stylosa* Desv., *R. suberecta* Ley. × *mollis* Sm. and *R. suberecta* Ley × *coriifolia* Fr. In the absence of experiment it is impossible to confirm or contradict these determinations. The first two hybrids must be uncommonly

difficult to diagnose as such, since the supposed parents are so closely similar in many features. There is nothing improbable, however, in the supposition that closely allied species may hybridise just as freely as the species mentioned in the foregoing paragraphs. This theoretical consideration is of great importance and it bears very directly on the whole discussion which follows. If closely related species or species and varieties hybridise the hybrid origin of the offspring would be exceedingly difficult to detect. In actual practice they would not, as a rule, be distinguished as hybrids, but would be considered distinct species or varieties and would be named as such. Thus, perhaps, has arisen a large portion of the total number of named varieties of roses. It is exceedingly interesting to find, therefore, that Almquist, one of the most recent writers on the genus, treats *R. glauca* and *R. coriifolia*, two very closely related forms, as a collective species under the name *R. Afzeliana* Fr.= *R. glauca* × *coriifolia* (see Traaen, 1913).

On the general question of hybridism in the Rosaceæ the work of Jeffrey may be mentioned. "Not only are certain of the Rosaceæ recognisable as hybrids on account of their transitional features of organisation, Mendelian phenomena, etc., but certain others which have not revealed themselves as hybrids in these ways are clearly such as a result of a study of their spores. We have consequently to distinguish in the case of the Rosaceæ, if the morphological features are taken into account as well as the data of systematic botany, three kinds of individuals, namely, pure species, recognised species which from the condition of their pollen are in reality concealed hybrids or crypthybrids, and recognised hybrids." The subject, in so far as it concerns the genus Rosa, has been pursued by Miss Cole (1917) who, from a study of the pollen in numerous roses, concludes that the genus contains only a few pure species, while the great majority of so-called species are really of hybrid origin. Unfortunately, Miss Cole's investigation does not include many species native in Britain, and the condition of the pollen in British forms I hope to make the subject of a future paper.

It has already been mentioned that there is no experimental evidence to show whether the species-hybrids described above segregate or remain stable. It has generally been believed that only crosses between varieties segregate, but the work of Brainerd (1907) on American Violets points clearly to segregation in the offspring of species-hybrids. Brainerd found growing wild

numerous violets which he determined as natural hybrids between certain species. These plants were taken into cultivation and found to be more or less sterile, but the small number of seeds obtained from cleistogamic flowers gave rise to plants showing segregation in regard to several features. "It is certain," according to Bateson, "that segregation in countless instances plays a part in the constitution and maintenance of characters held by systematists to be diagnostic of species. One has only to glance over trays of birds' skins, the portfolios of a herbarium, or drawers of butterflies and moths to discover abundant 'species' which are analytical varieties of others. The principles of heredity we trace in our experimental breeding are operating throughout the natural world of species."

If segregation occurs in the genus Rosa, and it is difficult to believe that it does not occur, we might expect to find a large number of visually distinct forms showing various combinations of Mendelian unit characters such as hairiness, leaf serration, glandularity, glaucousness, etc. Moss (1912) has pointed out that the numerous forms of the highly variable species *Stellaria dilleniana* Moench. may be regarded theoretically as various combinations of several unit characters such as glaucousness or greenness, large or small petals and many-flowered or few-flowered cymes.

Before attempting to make a theoretical analysis of some of the British species of Rosa on the basis of a few separate characters such as have been mentioned, it will be useful first to indicate the groups into which the genus may be divided. For this purpose the following table, which presents the sections and groups more or less in accordance with the views generally held by systematists, has been drawn up.

It will be seen from the dates of publication included in brackets in Table I that the term "group" generally, though not always, corresponds to one of the older aggregate species. The numerous sub-species and varieties of these aggregates which have since been described I shall attempt to analyse as far as is possible on the basis of a few characters commonly employed by systematists for the differentiation of these forms.

Rosa arvensis Hudson, *Fl. Angl.* 1762, is the British representative aggregate species of the Section Synstylæ in which the styles are combined into a long slender column equalling the stamens. A number of forms (the term is used throughout in a

TABLE I.

Section I. Synstylæ.

Group of *Rosa arvensis* Huds. (1762).

Section II. Stylosæ.

Group of *Rosa stylosa* Desv. (1809).

Section III. Caninæ.

Sub-sect. Eu-caninæ.

Group of *Rosa canina* Linn. (1753).
„ „ *dumetorum* Thuill. (1799).
„ „ *glauca* Vill. (1809).
„ „ *coriifolia* Fries (1814).
„ „ *subcanina* Chr. (1873).
„ „ *subcollina* Chr. (1873).
„ „ *tomentella* Lém. (1818).

Subsect. Rubiginosæ.

Group of *Rosa Eglanteria* Linn. (1753).
„ „ *micrantha* Sm. (1812).
„ „ *agrestis* Savi (1798).

Subsect. Villosæ.

Group of *Rosa villosa* Linn. (1753).
„ „ *tomentosa* Sm. (1800).

Section IV. Pimpinellifoliæ.

Group of *Rosa pimpinellifolia* Linn. (1753).

Section V. Pimpinellifoliæ Hybridæ.

Group of *Rosa involuta* Sm.
(*R. pimpinellifolia* agg. × *tomentosa* agg.)
Group of *Rosa hibernica* Templ.
(*R. pimpinellifolia* agg. × *Eu-caninæ*).
Group of *R. biturigensis* Bor.
(*R. pimpinellifolia* agg. × *rubiginosa* agg.)

general sense only) may be distinguished according to leaf-serration and the nature of the peduncles. To take these two characters only, (1) Biserrate leaflets (B), not biserrate (b), (2) Hispid, glandular or setose peduncles (S), smooth peduncles (s), the following four theoretical combinations may be expected—BS, Bs, bS, and bs. *R. arvensis* Huds. is a bS form and the smooth peduncled form bs is *R. erronea* Rip. The combination BS corresponds to var. *biserrata* Crép. This analysis does not include *R. ovata* Lej. which is simply a narrow-fruited variety of the type, nor *R. gallicoides* Déségl. a fairly well-marked form owing to the admixture of acicles on the upper part of the stems, a feature which

may possibly indicate that *R. pimpinellifolia* may have entered into the plant's composition through hybridisation. By some authors *R. gallicoides* is regarded as *R. arvensis* × *gallica*.

Rosa stylosa Desv. in *Journ. de Bot.* 1809, is the only aggregate species of the Stylosæ section, a group which is unquestionably intermediate in its general features between the Synstylæ and the Eu-caninæ, some authors including it in the former section while others place it in the latter. This intermediate position immediately suggests hybridisation between Synstylæ and Eu-caninæ forms in the production of those forms which constitute the Stylosæ. The distribution of *R. stylosa* agg. is the same as that of *R. arvensis* agg., while Eu-caninæ forms of the group *dumetorum* are widespread and it is from this group of the Eu-caninæ that some members of *R. stylosa* are almost indistinguishable. It might be interesting and instructive, therefore, to cross systematically *R. arvensis* and *R. dumetorum*.

In *R. stylosa* there is little variation in the serration of the leaflets, all the British forms being uniserrate except var. *evanida* Chr. which is biserrate. But the leaflets in some are hairy (H), in others glabrous (h). Forms with rose-coloured (R), others with white (r) flowers occur, while some have setose (S), others smooth (s) peduncles. If we deal with those three characters only, the following eight combinations would be visibly different—HRS, HrS, HRs, Hrs, hRS, hrS, hRs and hrs. At least five of these combinations have been met with in Britain and are known by distinctive names. The type of *R. stylosa* Desv. is the form HrS, while HRS corresponds to *R. systyla* Bast. Hrs is *R. stylosa* var. *corymbosa* Desv. = var. *opaca* Bak. and var. *pseudo-rusticana* Crép. is the combination hrS. *R. virginea* Rip. comes under the hrs combination. Only one form with rose-coloured flowers is included in this analysis, but another, viz. *R. parvula* Sauz. et Maill. occurs on the Continent and has been reported as occurring in Britain. It corresponds to the combination HRs.

We pass now to Section III which is a very large one, the subsection Eu-caninæ itself containing by far the largest number of our British species and varieties. In general, the members of this subsection can be distinguished by their large size and arching habit, their uniform and decidedly hooked prickles and by the styles being free, at least not agglutinated into a column like those of Synstylæ and Stylosæ. Since the division into groups given in Table I is not that most usually adopted by systematists

a few notes on the arrangement may be useful. The group *canina* includes that large assemblage of forms characterised by the possession of glabrous leaflets, glabrous or slightly hispid styles, late-ripening fruit and reflexed sepals which disarticulate before the fruit changes colour. The group *dumetorum* is the exact counterpart of *canina* except that its leaflets are more or less pubescent. Its numerous forms may be grouped together as an aggregate species, *R. dumetorum* Thuill. or they may be regarded simply as hairy-leaved varieties of *R. canina*.

R. glauca Vill. and *R. coriifolia* Fr. are distinct and clearly defined from *R. canina* and *R. dumetorum*. Their members develop ascending or erect sepals which are subpersistent, not falling until the ripening of the fruit. Moreover, the fruit ripens earlier than in *canina* or in *dumetorum*. The styles, which are never much exserted, form a dense hemispherical mass, strongly hispid or woolly, a character by which it is nearly always possible to distinguish members of *R. glauca* and *R. coriifolia* from those of *R. canina* and *R. dumetorum*. *R. glauca* comprises glabrous forms; in *R. coriifolia* the leaflets are hairy. I regard the four groups as constituting two sets of parallel series of forms. The first two are generally distributed throughout Britain while the third and fourth are confined to the north of England and to Scotland.

The four groups have been fairly fully worked out systematically and a large number of forms have been described and named. No attempt will be made to give an exhaustive analysis of all these forms based on many characters, but in Table II the primary divisions of the groups are shown and it will be seen that the characters used are the serration of the leaflets, the presence or absence of subfoliar glands, the development or non-development of hispid peduncles. To these must be added, of course, the pubescence of the leaves as the distinguishing feature of *R. dumetorum* and *R. coriifolia* from *R. canina* and *R. glauca* respectively. The primary divisions of the four groups have been named in the table as if they corresponded to species, and while this is true for some, it has to be mentioned that others were described by their authors as varieties only. It is clear, however, that if the four groups are treated as equal in value, all the names which correspond to parallel divisions of the groups should also rank equally; whether we call them species or varieties is a matter of individual opinion.

TABLE II.

Group.	*R. canina.*	*R. dumetorum.*	*R. glauca.*	*R. coriifolia.*
Leaflets uniserrate				
Peduncles smooth	*R. lutetiana* Lém. ...	*R. urbica* Lém.... ...	*R. Reuteri* God. ...	*R. incana* Kit. ... ...
,, hispid...	*R. andegavensis* Bast....	*R. Deseglisei* Bor. ...	*R. transiens* Gren. ...	*R. bovernieriana* Lagg. et Pug.
Leaflets biserrate				
Eglandular beneath				
Peduncles smooth	*R. dumalis* Bechst. ...	*R. arvatica* Bak. p.p....	*R. subcristata* Bak. ...	*R. Watsoni* Bak. ... ...
,, hispid...	*R. verticillacantha* Mér.	*R. aciculata* Rouy. ...	*R. fugax* Gren. ...	*R. cæsia* Sm. ... ...
Glandular beneath ...				
Peduncles smooth	*R. scabrata* Crép. ...	... ...	*R. stephanocarpa* Rip. ...	*R. Lintoni* Scheutz. ... ...
,, hispid...	*R. Blondæana* Rip. ...	... ...	*R. œnensis* Kell. ...	*R. Bakeri* Déségl. ... ...

If we make an analysis on the basis of (1) hairiness of the leaflets (H), glabrousness (h), (2) biserration (B), not biserrate (b), (3) the presence of glands on the leaflets (G), the absence of foliar glands (g), (4) hispid peduncles (S) and smooth peduncles (s), then there are sixteen theoretical combinations to consider:—HBGS, HBGs, HBgS, HBgs, HbGS, HbGs, HbgS, Hbgs, hBGS, hBGs, hBgS, hBgs, hbGS, hbGs, hbgS, and hbgs. We may apply these combinations first to the *canina-dumetorum* groups; the last eight containing h will be glabrous and thus correspond to *canina* forms. Six of the eight combinations have been named. *R. lutetiana* Lém. is the form hbgs,, and *R. andegavensis* Bast. corresponds to the hbgS form. The combination hBgs covers *R. dumalis* Bechst., while similar plants with hispid peduncles come under the hBgS form, known as *R. verticillacantha* Mér. The two biserrate "species" with subfoliar glands are *R. scabrata* Crép. and *R. Blondæana* Rip., the former with smooth peduncles, *i.e.* hBGs, the latter with hispid peduncles, *i.e.* hBGS. The combinations hbGS and hbGs are without names. Four of the eight combinations containing H have been met with in Britain and comprise the series of forms which are classified under the *dumetorum* group since the leaves are hairy. The Hbgs form corresponds to *R. urbica* Lém., and to the HbgS combination the name *R. Deseglisei* Bor. applies. Of the biserrate hairy forms, *R. arvatica* Bak. p.p. corresponds to HBgs, while the HBgS combination is referable to *R. canina* var. *aciculata* Rouy. Four forms having subfoliar glands, HBGS, HBGs, HbGS and HbGs, are so far not recorded. It will be seen, therefore, that of the sixteen theoretical combinations of the four selected separate characters ten have been named, six of them falling under the *canina* group, the remaining four being *dumetorum* forms. These ten names do not exhaust the list of British roses which are classified under the *canina-dumetorum* series. Under *R. lutetiana*, for example, nearly a dozen named forms which may be distinguished according to size and colour of leaflet, shape of fruit, etc. are mentioned in Wolley-Dod's "List." It is not improbable that these are important characters, perhaps more important than the presence or absence of glands on the leaves or peduncles, but the data regarding them is so incomplete for so many named varieties that it has been impossible to include them in the present analysis. In any case, the employment of more than a few unit characters would lead to unnecessary complications.

We may pass now to the *glauca-coriifolia* groups and proceed to an analysis precisely similar to that which has been applied to the *canina-dumetorum* series. If we take first the eight combinations which include h, *viz.* hBGS, hBGs, hBgS, hBgs, hbGS, hbGs, hbgS and hbgs, we shall be dealing with *glauca* forms. The combination hbgs is *R. Reuteri* God. and the hispid-peduncled form hbgS is *R. Reuteri* var. *transiens* Gren. *R. subcristata* Bak. is the form hBgs and *R. fugax* Gren. corresponds to hBgS. The biserrate forms with subfoliar glands are hBGs and hBGS, the former combination having been named *R. stephanocarpa* Déségl. et Rip., the latter being *R. glauca* var *œnensis* Kell. Only two of the eight combinations remain unrecognised, namely hbGS and hbGs. Turning now to the eight combinations having H in their composition, *viz.* HBGS, HBGs, HBgS, HBgs, HbGS, HbGs, HbgS and Hbgs, we find that six have been named. These, of course, come under the *coriifolia* group. *R. incana* Kit. is an Hbgs form and constituted the type of Fries. The combination HbgS is *R. bovernieriana* Lagg. et Pug. *R. Watsoni* Bak. and *R. caesia* Sm. correspond to the forms HBgs and HBgS respectively. The combination HBGs applies to *R. coriifolia* var. *Lintoni* Scheutz and the counterpart with glandular peduncles, HBGS, is *R. Bakeri* Déségl. Thus, in the *glauca-coriifolia* groups, twelve of the sixteen theoretical combinations have been discovered and have received distinctive names. Unfortunately, an analysis on the basis of glaucousness and non-glaucousness or greenness cannot be attempted since the distribution of these characters in all the forms of the two groups is not known. But these characters are unquestionably important ones, and they receive much emphasis in Almquist's classification of Swedish roses to which reference will be made later.

The names *R. subcanina* and *R. subcollina* date from 1873 when they were used by Christ in *Rosen der Schweiz*, the former to describe a variety of *R. Reuteri* (glauca), the latter as a variety of *R. coriifolia*. By some authors they are still regarded as varieties or sub-species, but there are certain advantages in treating them as independent groups equal in value, from the point of view of the systematist, to *R. glauca* and to *R. coriifolia*. Already, evidence is accumulating to show that they probably each comprise a series of forms developing along lines parallel to those dealt with for the two aggregate species of which they were respectively described as varieties. The type of *R. subcanina* (Chr.) is a uniserrate form, but

a biserrate form, *R. glauca* var. *denticulata* Kell., has been recognised. *R. subcollina* (Chr.), as at present understood in this country, is a slightly larger group, and includes the type of Christ, which is uniserrate, and at least three biserrate forms, *viz. R. subcoriifolia* Barclay, *R. cæsia* var. *incana* Bor. and *R. pruinosa* Bak. It would be possible to make an analysis of the *subcanina-subcollina* series on the lines already followed for preceding groups, though a considerable number of combinations would stand without names. But since the groups have not been at all fully worked out, it does not follow that the combinatious do not occur in nature. *R. subcoriifolia* Barclay is in itself a somewhat aggregate species. Its commonest form has subfoliar glands and smooth peduncles, and is thus an HBGs form, corresponding to var. *Lintoni* of the *coriifolia* group. But HBgs and HBGS combinations have also been met with, although they have not received distinctive names.

I have, however, a suggestion to make regarding the *subcanina-subcollina* series. *R. subcanina* is, in a number of features, intermediate between *R. glauca* and *R. canina*. Christ, in his description of the plant, remarks that it connects the two. In the possession of reflexed or downwardly spreading sepals it comes near *R. canina*, but in the woolly head of styles it bears a closer resemblance to *R. glauca*. In the length of the peduncles, the time of ripening of the fruit, and the persistence of the sepals it is more or less intermediate between *R. glauca* and *R. canina* and one is tempted to ask if *R. subcanina* may not be a hybrid between these two species. Again, *R. subcollina* as an aggregate is more or less intermediate in its characters between *R. coriifolia* and *R. dumetorum*. It holds an essentially similar position between these two aggregate species as *R. subcanina* does for *glauca* and *canina*, and one wonders if it, also, is not of hybrid origin. Experimental work is here extremely desirable. So far, as I am aware, there is nothing in the geographical distribution of these forms against the theory here suggested. Both *R. subcanina* and *R. subcollina* are most frequent in Scotland, becoming much rarer in the north of England, and they are quite absent in the south. Their distribution thus follows very closely that of *glauca* and *coriifolia*. *R. canina* and *R. dumetorum*, are, of course, abundant and widespread. It is noteworthy, also, that the two suggested hybrids, while they have the same distribution as *R. glauca* and *R. coriifolia*, are rarer than either of these two species.

There remains the group *R. tomentella* Lém. of the subsection Eu-caninæ. This is a small group, but a somewhat difficult one to segregate. Typical examples, possessing sub-orbicular, pubescent leaflets, more or less glandular beneath, and hard late-ripening fruit with reflexed sepals, are fairly easily recognised, but "some individuals," to quote Wolley-Dod, "are liable to be mistaken for members of *Tomentosa*. Its more glandular members also run near forms of *Micrantha* while those with eglandular leaflets are often very difficult to distinguish from the group *Dumetorum*." The limits of the group are thus extremely ill-defined and it is not improbable that some of its members owe their indefiniteness to hybridisation with forms belonging to other groups. We may, however, attempt an analysis on the basis of leaf-serration (Bb), glandular or eglandular leaflets (Gg) and hispid or smooth peduncles (Ss). The following eight possible combinations have therefore to be considered: – BGS, BGs, BgS, Bgs, bGS, bGs, bgS and bgs. The type of *R. tomentella* Lém. is a BGs form, the variety with hispid peduncles, BGS, being var. *decipiens* Dum. An eglandular variety, the combination Bgs, may be placed, according to Wolley-Dod, in *R. carionii* Déségl. et Gill. although Déséglise himself regarded this as a *dumetorum* form. Of uniserrate forms, *R. obtusifolia* Desv. corresponds to the combination bGs, and the only other uniserrate member is *R. canina* var. *concinna* Bak. which closely resembles *R. obtusifolia*, but having hispid peduncles, it represents the combination bGS. Three of the eight combinations have not been named, BgS, bgS and bgs. If they did occur in nature they would be extremely difficult to distinguish from members of the group *dumetorum* since they are all eglandular forms.

We now pass to the subsection Rubiginosæ, the members of which can be distinguished from those of the Eu-caninæ primarily by the abundance of subfoliar scented glands. The subsection includes three groups which may be named after the aggregate species *Eglanteria* L., *micrantha* Sm. and *agrestis* Savi.

Comparatively small, more or less tufted plants, are characteristic of the group *Eglanteria*. The stems show small acicles mixed with the main prickles, which are hooked and curiously uncinate in shape, quite different from the type of prickle generally seen in Eu-caninæ forms. Whether this mixed armature is any indication of hybridity in the group as it certainly is in the case of *R. involuta* and *R. hibernica*, I am unable to say, but it is of considerable interest to note that Miss Cole found only 10% fertile

pollen in *R. rubiginosa* (*R. Eglanteria*), this remarkable pollen-sterility being attributed to hybridisation. All the British forms of *R. Eglanteria*, except *var. jenensis* Schulze, have strongly hispid peduncles, and are usually differentiated according to whether the main prickles are distinct from or gradually merge into the acicles and by the ultimate direction and relative persistence of the sepals. All these varying features may be the result of various crossings, although I am at present quite unable to suggest a possible parentage for the aggregate *R. Eglanteria.*

The members of the small group *micrantha* show a taller and more arching habit recalling that of *R. canina* L. The stems do not present any admixture of acicles with the main prickles. The peduncles are glandular hispid in all the British forms except var. *Briggsii* Bak. *R. Hystrix* Bak. may be distinguished from the type and from *var. permixta* Déségl. by its smaller leaflets, while the type may be distinguished from the last-mentioned form by the absence of prickles from the flowering branches.

The group of *R. agrestis* is also a small one and runs very close to that of *R. micrantha*, its members differing primarily in having smooth peduncles. They are small leafleted forms and it does not appear possible to segregate them satisfactorily, except perhaps on the basis of leaf pubescence, the presence of which marks off *R. sepium*, var. *pubescens* Rouy from the type of *R. agrestis* (=*R. sepium* Thuill.) which has glabrous leaflets.

The sub-section Villosæ may be regarded as comprising two groups only, one corresponding to *R. villosa*, L. of which *R. mollis* Sm. is the representative species in Britain, the other group being known under the name of *R. tomentosa* Sm. The members of the two groups vary considerably in habit, from low erect bushes to large, arching forms. The prickles are uniform, slender as a rule, straight or somewhat falcate. The leaflets are biserrate, very hairy, often softly tomentose and generally glandular, often decidedly so as in Rubiginosæ forms, but the glands have a resinous not a fragrant odour.

R. mollis Sm. is a tolerably well-defined species, at least as an aggregate, reaching its greatest frequency in the North of Britain. It varies chiefly in the amount of glandular development of the leaves and in the hispidity of the peduncles. To take these two characters only, we find that all the four theoretical combinations have been recognised, GS, Gs, gS, and gs, three of them having been named. The form gS, may be regarded as the type of *R.*

mollis Sm. while the combination gs, applies to the var. *cærulea* Woods. The GS form is *R. pseudo-rubiginosa* Lej. This leaves the combination Gs unnamed, but such forms are not unknown and have been frequently noticed occurring with the other varieties.

The group *tomentosa* is a more difficult one to deal with. It is usual, in this country at least, to divide it into three sub-groups according to the direction and relative persistence of the sepals. In *R. omissa* Déségl. the sepals ultimately become quite erect and persist until the fruit is ripe. On the other hand, the third sub-group, represented by *R. scabriuscula* Sm., includes those forms characterised by the possession of reflexed and early-deciduous sepals. An intermediate sub-group is that of *R. subglobosa* Sm.=*R. Sherardi* Davies, in which the sepals are spreading or no more than slightly ascending and they disarticulate before the fruit is fully ripe. The whole group is perhaps the most difficult one we have to classify and it would not be surprising to find that this difficulty is largely due to hybridisation and re-hybridisation among the different forms. An experimental investigation to discover whether *R. subglobosa* Sm. is not, in fact, a hybrid between *R. omissa* Déségl. and *R. scabriuscula* Sm. would be exceedingly valuable.

We come, finally, to the section Pimpinellifoliæ containing *R. pimpinellifolia* L. which is one of the best-defined and perhaps least variable species we have. Essentially a plant of sandy sea-coasts, it is nevertheless not unknown from inland stations. Its habit, setigerous stems, and distinctive foliage are features which at once distinguish it from other members of the genus. If we consider leaf serration and the nature of the peduncles, using the same letters as before, then, of the four combinations, BS, Bs, bS, and bs, the last-mentioned is the commonest form and applies to *R. pimpinellifolia*. The bS form corresponds to *R. spinosissima*. The only variety with fully biserrate leaflets is *R. Ripartii* Déségl. which corresponds to the combination Bs. In Britain this plant is somewhat rare, but a faint biserration is fairly frequently seen in the type. Well-defined forms of the BS combination have not been recognised, although forms approaching it have been recorded without any distinctive name.

In the theoretical analysis which has been attempted in the foregoing pages comparatively few characters have been taken into consideration. The selection of a few has been deliberate, as my main purpose has been rather to direct attention to the very high

probability of the presence of various combinations of Mendelian unit characters in the several groups than to give an extensive and involved analysis on the basis of a large number of separate characters. The argument throughout is, of course, entirely hypothetical and experimental results are required to establish the hypothesis. It is impossible to over-emphasise the need for cultural work, so intensive has the study of British plants become, and, as already pointed out, morphological methods alone are insufficient for the complete solution of the intricate problems involved. Yet, it is remarkable how little has been done to discover experimentally the genetic relationships within our numerous "critical species" and genera. The work of Trow (1912) on *Senecio vulgaris* Linn. clearly points to the need for similar studies on other aggregate species.

Almquist, whose work has already been mentioned, makes a very interesting attempt in his account of *Rosa*, in Lindman's *Svensk Fanerogamflora* (1918) to refer the micro-forms of the genus ultimately to certain characteristic types which are based on the following characters:—glaucousness, greenness, glabrousness and hairiness. "Species" with glaucous leaflets are referred to *gl.* (*glauca*) if they are glabrous, to *glf.* (*glauciformis*) if the leaflets are hairy. Green-leafleted "species" are referred to *vir.* (*virens*) if the leaflets are glabrous, to *virf.* (*virentiformis*) if hairy. This plan is applied throughout the eight sections and thirty-one species-types into which the genus has been divided. Thus, any rose whose sectional and type characters have been determined finds a place in Almquist's scheme according to whether it is a *gl.*, *glf.*, *vir.*, or *virf.* form. This method of segregation has involved the creation by Almquist of a large number of new names, especially in the Afzeliana *(R. glauca* × *coriifolia)* and Caninæ sections, where combinations of these characters are apparently frequent. But it is the scheme itself which claims one's attention and interest. Almquist contends that the chief characters in classifying roses are the colour and consistence of the leaves, the form of the leaflets and the shape and direction of the teeth. He pays little attention to the direction of the sepals, while biserration, the development of glands, etc., are regarded as modifications of primary types. There is much in favour of Almquist's views and I think his method must result at least in bringing together similar-looking plants. *R. lutetiana* and *R. dumetorum*, for example, find a place side by side in the Caninæ section under species-type *cuneatula*, the former a *vir.* form, the latter a *virf.*

The need for some such system in dealing with our British Roses is obvious, but an entirely new classification should not be attempted until the support of experimental evidence is forthcoming. Cultural results will not be obtained without the expenditure of much time and patience, but even if a single aggregate species like *R. canina* L. were submitted to systematic crossing and fully worked out along the lines of Mendelian research, we should obtain results, I think, which would form a real contribution to our knowledge of this most difficult genus.

I do not wish, at present, to enter very far into the controversy as to how many names should be retained or how many more should be invented. If it be proved that elementary species arise and remain stable it may be desirable to name such forms as the natural units of classification, but in the present state of our knowledge, the creation of innumerable names in a genus like Rosa, seems to be devoid of all scientific principle and is much to be deprecated. I would at present strongly support any systematist who returned to the Linnean conception of the species, denoting its various combinations by some purely symbolical method.

In conclusion I wish to mention that the present contribution has grown out of a correspondence with Mr. A. G. Tansley, F.R.S., on some of the questions that have here been discussed, and I gladly take this opportunity of expressing my thanks to him for the great interest he has shown in its preparation.

Postscript.

Since the above paper was written Colonel Wolley-Dod has made a further contribution to the study of the genus under the title "A Revised Arrangement of British Roses," published in the *Journal of Botany*, 1920. The author has reached the conclusion that "most of the very detailed descriptions of Déséglise, Ripart and others can hardly be other than those of an individual bush or specimen, which cannot be completely matched by any other," and in consequence of his conviction of the worthlessness of nearly all the so-called species of these authors, he has reduced the number of names having full specific rank to eighteen. We find, for example, in the large subsection Eu-caninæ only five species—*R. lutetiana*, *R. Blondæana*, *R. dumetorum*, *R. Reuteri* and *R. tomentella*. It is true the author still retains a formidable list of names under most of the species, but these are never accorded more than varietal rank and many are regarded simply as forms.

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MUTATIONS AND EVOLUTION.

By R. Ruggles Gates.

CHAPTER VI.

Presumptive Mutations in Wild and Cultivated Plants.

OBVIOUSLY, if the mutation theory is to be of any use the conceptions derived from controlled breeding experiments must be applicable to plant and animal species and varieties as they occur in nature. A beginning has only been made in this vast field of application, but it is sufficient to show that the mutationist conception of germinal changes is widely applicable to the variations observed among wild species. As an aid in the analysis of the populations that go to make up a wild species it is undoubtedly of great service, and its illuminating influence is also beginning to make itself felt in the fields of systematics, phylogeny and relationships. Innumerable records of species, varieties and forms in the literature of systematic botany and zoology and the journals of naturalists show how universal is the incidence of this principle.

That the relationships and origin of nearly related species can also in many cases be most clearly interpreted in terms of unit differences has been shown by Bateson (1913) for the North American warblers (Helminthophila) and flickers (Colaptes) and other forms. In plants, the same principle has been applied (Gates, 1916) to species of Spiranthes, Clintonia, Streptopus, Maianthemum, Ranunculus, Actæa and Spiræa, and in a preliminary way to the genus Trillium (Gates, 1917b). Similar analytical conceptions have been applied to the differentiation of species and varieties, their relationships and phylogeny, in the North American Melanthaceæ (Gates, 1918a) and Convallariaceæ (Gates, 1918b). The results are in no sense revolutionary, but wherever the mutational principles are applicable they do appear to give a more clear-cut and accurate analysis of specific differences, and also of the phylogenetic and distributional relationships within a group. Moreover, there is the beginning of a physiological element in classification on these principles, which is a distinct gain. More recently Small (1917-19) has successfully applied these principles to a study of the development of the Compositæ.

It is obvious that in older groups, and wherever extinction has taken place, the actual succession of mutations in the development of any group will be obscured or lost altogether. These principles can be most readily and widely applied to modern expanding groups

in which the origin of new divergent characters is now or has recently been taking place.

Turning now to the recorded cases of mutation in the literature, they form such an array that it would be a colossal task to attempt even to enumerate them. The condition is so common in flowering plants that it may be considered exceptional to find a species without any mutational varieties. A few instances will be selected, almost at random, for mention here. First we will consider doubling.

Doubling.

The gardeners' tradition that "doubling" or the transformation of stamens into petals,[1] is a result of cultivation has long been disproved. It is evident from the records that doubling of flowers occurs "spontaneously" both in wild and cultivated species. It is a typical mutation, although the completeness of the transformation of stamens into petals, and the associated changes in the flower, may vary in different cases. Breeding experiments have shown that the double condition is in some forms a Mendelian dominant, but more usually a recessive. Bateson (1909, Chap. XI) has considered the cases studied before 1909. The work of Miss Saunders on the inheritance of doubleness has been most ample, and some of her results may be summarized here. Taking the simpler cases first, she finds (1917) that in the Welsh poppy, *Meconopsis cambrica*, doubleness is dominant, the F_2 from a cross containing three doubles to one single. The doubleness results from a variable degree of petalody of the androecium and gynœcium. In the hollyhock (*Althæa rosea* and *A. ficifolia*) the F_1 is intermediate and the F_2 gives the 1 : 2 : 1 ratio, *i.e.*, neither condition dominant; in carnations (*Dianthus caryophyllus*) doubleness is a simple dominant,[2] while in sweet william (*D. barbatus*) singleness is dominant and the F_2 from a cross contains three singles to one double.

In *Chelidonium majus* Sax (1918) finds that doubleness is apparently a simple recessive, but the F_2 gives a continuous series from singles to full doubles. Statistically considered, there is much

[1] Doubling may also occur, as in Fuchsia, by an increase in the number of petals without any change in the stamens, or it may result from change of carpels to petals, or from all these conditions combined.

[2] According to the breeding work of Norton and of Batchelor the doubleness of carnations appears to be of two distinct types or degrees, full doubles and standard doubles, the latter having some stamens. Full double × single gives an F_1 which is standard double, and an F_2 with the three types in the ratio 1 : 2 : 1. Miss Saunders finds, however, all degrees of doubling in the DD's and DR's, which are therefore indistinguishable.

greater variation in the doubles than in the singles, and a high negative correlation between petal number and stamen number in F_2 plants, as would be expected if stamens are replaced by petals.

The more complicated cases of doubling have been elucidated by the well-known work of Miss Saunders on Petunia (1910, 1916a, 1916b), Matthiola (1911, 1913, 1915a, 1915b), and the wall flower *Cheiranthus cheiri* (1916c, 1917). According to Frost (1915), doubleness is dominant in Petunia, and Miss Saunders (1916b) concurs in this statement to the extent of finding that all true-breeding singles of *P. violacea*, *P. nyctaginiflora* and various garden strains, when pollinated from doubles give an F_1 containing both singles and doubles. This indicates the heterozygous character of the doubles, and hence the dominance of doubleness over singleness. But since the doubles are sterile and *P. violacea* itself is a self-sterile species it has not yet been possible to eliminate the possibility that singleness is dominant, though Frost's hypothesis of selective sterility accompanied by dominance of doubleness would appear to fit the facts. In the wallflower, as in sweet william, singleness is dominant.

In the case of Stocks (Matthiola) the prolonged experiments of Miss Saunders have gone far to clear up the hereditary relationships. Singleness is dominant, and it is well-known that in the various strains both pure-breeding and double-throwing (eversporting) singles occur. The inheritance of singleness or doubleness is independent of the pair of Mendelian characters for hoariness or smoothness, and also of cell-sap colour, but is linked with plastid colour (whether white or cream). All the singles derived from an eversporting individual appear again to throw doubles. And in all cases there is an excess of doubles in the offspring in the ratio of something more than 7 singles : 9 doubles, from which it is concluded that two factors are primarily concerned in producing a single or a double.

Moreover, breeding experiments show that all the functional pollen grains of eversporting individuals carry doubleness, while some of the ovules carry the factor for doubleness, and some that for singleness, in the above proportion. Miss Saunders (1911) explained the absence of doubles in the offspring of true-breeding singles when crossed together, by an unequal distribution of the factors among pollen grains and ovules. In the light of more recent work it is probably simpler to explain the fact that some singles breed true by assuming linkage of one determiner to a lethal

factor. This does not of course explain the important fact of differential viability of certain types of gametes as between pollen and ovules.

Miss Saunders assumes that singleness in stocks is due to the presence of two factors X and Y, that in the eversporting singles these two factors show partial coupling, and that they are both carried only by the ovules. Also a factor W represents colourless plastids, while in cream forms that breed true W is absent. There is also a sulphur-white race, heterozygous for W, in which W is present in some of the ovules but absent from the functional pollen. This relationship appears to be explained by coupling of W with either X or Y. Again, in the singles which breed true for singleness it is assumed that X and Y are linked, so that in crosses with eversporting singles recombinations cannot occur. These complicated relationships of factors are quite in harmony with results obtained from breeding experiments with other organisms.

Another feature of the double stocks is that they show greater viability than the singles, and hence appear in a higher percentage from old seed and also when the more vigorous plants are selected before flowering.

The various varieties of stocks must have originated through mutations, and Miss Saunders (1915b) traces the historical order of their appearance.

In Fuchs' herbal (1542) the purple, red and white forms were already known, but Ruellius a few years earlier makes no mention of the red. The purple and white varieties of *Matthiola incana* date back to Dioscorides. The first record of the double stock appears to be in Dodoens' herbal (1568). This is also the first European record of the double wallflower. Double violets are apparently first mentioned in a work published in 1535.

The records indicate that the double stock perhaps originated in cultivation in some Dutch garden, and they show that it was completely double and sterile from its first appearance—no doubt a mutation. Sowerby (*Eng. Bot.*)[1] figures a hoary stock obtained from the cliffs of Sussex in 1806. This shows partial doubling in some flowers. The species must have independently developed a factor for doubling in this locality.

Frost (1912) describes an "early" dwarf mutation with few nodes from ten-weeks stocks. It is said to behave as a simple Mendelian dominant, but the evidence is not very clear.

[1] See Saunders (1917).

A much earlier record of a double wallflower has, however, since been found (Saunders, 1916c). There is a reference to it in an Arabic "Book of Agriculture" of the 12th Century, the statements in which are based on an earlier work probably written about 1073. As we shall see, the records show that doubling is by no means rare in wild species, so it is quite possible that a double wallflower was taken into cultivation as such. Doubling appears to have occurred at least twice in cultivation. The older, fully double wallflower (Saunders, 1917) was wholly sterile like the double stocks. It appears to have originated only once as a sport, and have since been propagated by cuttings. The partial double is more recent in origin and shows grades of doubling forming a continuous series. This double form is therefore not in the same series with the full double, but represents an independent germinal change.

Bateson and Miss Sutton (1919) have found greater irregularity in Begonia. A double monœcious ♀ × single ♂ gave singles generally dominant, but segregation was irregular and transitional forms appeared. An average of 1 double in 32 was obtained, and back crosses were also irregular. *B. Davisii* from Peru crossed on common doubles gave only double. This single is believed to be genetically double on the ♂ side.

The first double Dahlia is mentioned and figured in a work on the natural history of Mexico, published at Rome in 1651.[1] Hence it apparently did not originate in cultivation. There are a number of early American records of wild species with double flowers, some of which may be summarized here. In *Saxifraga Virginiensis* we have found nine records of double flowers, as follows: (1) A double found near Hingham, Mass., in 1849.[2] (2) Asa Gray[3] found a double at Dawers, Mass., 1866, which continued so from year to year. (3) A specimen found on the Delaware River below Easton with extra petals.[4] This was apparently not fully double. (4) A wild double from Canaan, Conn., was reported by A. Gray.[5] It bore 70 or 80 flowers, all pure white and fully double, without stamens. This very ornamental plant was divided, and part of it cultivated in the Cambridge, Mass., Botanic Garden. (5) Two more specimens were found[6] on the banks of the Schuylkill, near

[1] Gard. Chron. 59: 336, 1916.

[2] J. L. R., Amer. Nat. 2: 610, 1869.

[3] Amer. Nat. 2: 484, 1869.

[4] Porter, Thos. C., Bot. Gazette 1: 5, 1875.

[5] Amer. Nat. 11: 366, 1877.

[6] Martindale, I. C., Amer. Nat. 11: 432, 1877.

Philadelphia, having larger flowers than in the previous case. (6) Meehan[1] records finding a double on the Wissanickon about 1854. (7) One near Beverly Bridge, Mass.,[2] with panicle smaller than normal, the flowers full double, petals replacing both stamens and pistil. (8) Meehan[3] reported a double from North Woburn, Mass. These records, through trivial enough in themselves, acquire interest when considered as a whole. For they show that in a large part of its area and for over a quarter of a century *S. Virginiensis* was producing sporadic doubles as mutations. It is probably doing so still, and it may be that, as in stocks, some individuals are eversporting, giving rise to fresh doubles in each generation.

Before leaving Saxifraga we may point out some of the other derivative forms which have been described in this genus. Sterns[4] describes a form of *S. Virginiensis* on Manhattan Island which he called var. *pentadecandra*. In two plants observed nearly all the flowers had 15 stamens, the extra 5 replacing the petals. In these apetalous flowers the stamens were exposed in the bud. Such a change of petals to stamens is relatively rare. Several other plants in this location had apetalous flowers, but the stamens were ill-formed and more or less aborted. Three more specimens were found[5] in the locality in the following year. The same variation occurs in the cultivated European species *S. granulata*, as recorded by Masters.

This must be regarded as a case of parallel mutations. In *S. crassifolia* an abnormal increase in the number of pistils has been repeatedly observed, while *S. Virginiensis* var. *chlorantha* Oakes was described from Topsfield, Mass., 1847, having tiny green pubescent petals.[6] Var. *pentadecandra* was found in profusion in a slate rock locality in Essex Co., Mass. The Saxifrages are evidently subject in the wild condition to many mutations besides doubling.

Thalictrum anemonoides is another species for which there are a number of records of doubling. A semi-double found near Cincinnati, Ohio, in 1834 was taken into cultivation and in five years

[1] Amer. Nat. 2: 484, 1869.

[2] Russell, J. L., Am. Nat. 3: 327, 1869.
Amer. Nat. 6: 487, 1872.

[4] Sterns, E. E. Some anomalous forms of *Saxifraga Virginiensis*. Bull. Torrey Bot. Club 14: 122—125, 1887.

[5] Bull. Torrey Bot. Club 15: 166, 1888.

[6] See also Rhodora 19: 143, 1917.

produced full double flowers.[1] Many other instances of doubling in this species are on record from Asa Gray, Thomas Meehan and others. Doubles are also recorded in many species of Ranunculus. Thus *R. rhomboideus* is sometimes found double in Floyd Co., Iowa.[2] One such specimen was transplanted and continued to produce only double flowers. A specimen of *R. repens* L. collected near Camden, New Jersey, had 10 petals (an extra whorl).[3] *R. multifidus* Pursh at Grand Rapids, Mich., frequently has double and quilled flowers, often with the scales (nectaries) changed to tubular appendages.[4] *R. acer*, *R. bulbosus* and *R. ficaria* are all said by Meehan[5] to have double forms. He points out that doubling is rarely due to cultivation, although numerous double forms of Ranunculus now occur in seed catalogues.

Records of doubling in the Canadian mayflower, *Epigæa repens*, also abound, though the change is not so regular as in other forms, there being great variation in the nature of the doubling. A specimen from Worcester, Mass., continued to produce doubles for several years.[6] The stamens were partly converted into petals, the outer series being more or less coalescent into a tube. Other records are from New Brunswick and Massachusetts, the latter being a specimen with flower having three corollas, one within the other, the stamens absent or abortive.[7] At Plymouth, New Hampshire, double flowers were observed[8] year after year, with great variation in the degree of doubling. Three-fourths had two whorls of 5 petals each, and 5 stamens alternate with the inner petals. In a few flowers nearly all the 10 stamens were transformed into petals, and in all the carpels were transformed to leaves.

In *Hepatica triloba* Gil. one specimen with strongly double flowers was found (Hilbert, 1913) near Sensburg, Germany, in 1894, surrounded by singles. In 1912 another double specimen with blue flowers was found in the same place. It was transplanted to a garden and flowered double the following year, but gave no seeds. The stamens were changed to petals. There is also in cultivation

[1] Amer. Nat. 2: 610, 1869.
[2] Arthur, J. C., Amer. Nat. 6: 427, 1872.
[3] Bot. Gazette 1: 5, 1875.
[4] Bot. Gazette 2: 90, 1877.
[5] Amer. Nat. 2: 484, 1869.
[6] A. Gray, Am. Nat. 6: 429, 1872.
[7] Bailey, W. W., Bot. Gaz., 6: 238, 1881.
[8] Wilson, Kate E., Bot. Gaz. 15: 19, 1890.

a strongly double red form. A double *Anemone Pulsatilla* is figured by Helwing as early as 1719. Doubling is well-known to be of frequent occurrence in the Ranunculaceæ. A *Convolvulus sepium* with double flowers is described from New Brunswick, New Jersey.[1]

An interesting record is that of *Sagittaria variabilis*,[2] Engelm., a large patch of which, on an island in the Susquehanna, had completely double flowers. All the carpels of pistillate flowers and all the stamens of staminate flowers were converted into petals, giving the flowers the appearance of tiny snowballs. This probably represented a single individual mutation which had spread from rootstocks Elsewhere (Gates, 1917b) we have assembled numerous records of doubling in *Trillium grandiflorum*, the same root stock producing each year a double flower. There are various interesting records of double wild Rhododendrons. Rehder (1907) found in the woods at Glacier, British Columbia, a bush of *R. albiflorum* Hook. with double flowers. It was growing among normal bushes. In the double flowers, petalody of the stamens was combined with an increase in the number of staminal whorls. In the Alps, *R. ferrugineum* has been observed at least twice with double flowers, Kerner having found a large number of such shrubs in one locality. Miyoshi (1910) has described the occurrence of doubles in *R. brachycarpum* Don. The double form is called var. *Nemotoi* Makino. In the location (on a volcanic mountain) where it was found both white and rose varieties occur, but only the white showed doubling. Seven plants were observed with double flowers and ten with normal. In another place a group of five bushes was found, all with double white flowers. Nakai[3] found double and white varieties of *R. Kaempferi* in the vicinity of Karume, Japan.

That cultivation does not produce doubling, even in a genus where doubles occur wild as mutations, is clear from the case of *R. Metternichii*, which is much cultivated in Japan but no double is known. If there is any relation between the environment and the occurrence of mutations in this genus, it remains elusive, as in most other organisms. We still have no better term than "spontaneous" to apply to it.

Makino[4] cites also the finding of one double *Oxalis corniculata*, and *Deutzia scabra* entirely double in a locality in Nikko.

[1] Bull. Torrey Bot. Club, 17 : 238, 1890.

[2] Porter, Thos. C., Bot. Gazette 1 : 5, 1875.

[3] Bot. Mag. Tokyo, 29 : 261, 1915.

[4] Journ. Coll. Sci. Tokyo, 1910.

In a study of the variations of tobacco in the East Indies, Lodewijks (1911) states that double flowers are the most common aberrations, although gigantism, fasciation and other types of change also occur. Doubles appear yearly on almost every plantation, and the doubling is of the hose-in-hose type. All parts of the plant are also changed, so that doubles can easily be distinguished before they come into bloom. The stem is zig-zag, shorter and not winged; the leaves are very small and thicker owing to local outgrowths on their ventral surface; the midrib is twisted, and the stigma shows similar growths, though to a less extent. All these peculiarities apparently result from a single mutation, and the type breeds true. In crosses with the normal the latter dominates almost without exception, and the F_2 gives a 3 : 1 ratio (46S : 10D, 306S : 105D). It is a curious fact that the heterozygotes were distinguishable from pure singles by their leaves having outgrowths on the underside. Thus of the 306 singles above, 204 were shown in this way to be heterozygous and 102 SS. Again, in the F_2 from single × double the ratio was 32S : 58DS : 31D. It is very interesting that in this set of mutant characters, the double flowers are wholly recessive and the leaf peculiarity at least partially dominant, though they behave as a unit in inheritance.

In a work on the mountain cherries of Japan, in which is embodied an elaborate study of the group of plants which plays such a prominent part in the national life of that country, Miyoshi (1916) recognizes four species, *Prunus serrulata* Lindl., *P. mutabilis* Miyos., *P. sachalinensis* (Fr. Schm.) Miyos., and *P. fruticosa* Miyos., and a very large number of forms, especially of *mutabilis* (65) and *serrulata* (68). Cultivated double varieties have been known for over a thousand years. A great number of forms have arisen in the intervening period, but only the best have been preserved and many old varieties have been lost. In Yoshino, the oldest and most famous cherry neighbourhood, trees have from time to time been planted from the neighbouring mountains for over a thousand years. At Koganei, near Tokyo, is the greatest assemblage of wild cherries, none of which show any influence of cultivation. There are three other main centres for cherry varieties, and many places noted for a local form or even a single tree, but the larger centres have been the source of new forms and races from time immemorial.

From a study of the early records, Miyoshi concludes that a large number of cultivated sorts existed two centuries ago, and has been largely added to during the last hundred years. The many forms which receive botanical names for the first time are distinguished by such features as leaf colour, flower colour, singles or doubles, fragrance, inflorescence, and pubescence. The multiformity of the group is comparable with that of the North American Cratægus, or with *Draba verna* or *Viola tricolor*, and the forms appear to have arisen as mutations. Seeds in most cases yielded a uniform offspring, but it seems possible that some mutational characters may have been transferred by crossing.

Peloria.

Peloria, or the sudden development of actinomorphic flowers in a zygomorphic species, has been studied most extensively in the Scrophulariaceæ where it occurs most commonly, although it is also found in the Labiatae, Leguminosae, Orchidaceæ and other families with zygomorphic flowers. It is of evolutionary interest because zygomorphy is supposed to have been gradually developed in relation to the visits of insects, while peloria is a sudden re-expression of symmetry.

Peloria behaves in part as a recessive character, is known to occur as a variation in numerous wild species, and in a few cases has become a specific character, indicating that in such cases zygomorphy is not essential for survival. De Vries[1] studied peloria in *Linaria vulgaris* for thirteen years and gives the literature of the subject up to the time of his work. He mentions *Mentha aquatica* as a species whose apical flowers are always peloric, and *Uropedium Lindenii*, found in Colombia, as the peloric form of *Cypripedium caudatum*. It is not impossible that the Ranunculaceous genus Aquilegia, with its five spurs, arose as a peloric mutation from a zygomorphic one-spurred ancestor. The increased number of nectaries should give it an advantage as regards insect visits.

The genetical studies of peloria appear to have been confined to the Scrophulariaceæ, but in this family the genera Linaria, Antirrhinum and Digitalis have given valuable results. The earliest discovery of a peloric condition in *Linaria vulgaris* was made by Zioberg in 1742. On an island near Upsala he found among the normal a plant bearing only regular flowers, and Linnæus described it under the name *Peloria*. There are numerous later records of

[1] The Mutation Theory, Vol. II.

the same wild mutation elsewhere. The flowers have five spurs and this type is now known as *peloria nectaria*. There is another type, *peloria anectaria*, in which the flowers are actinomorphic, but without spurs. Another race studied by de Vries, which he called *hemipeloria*, produces usually a single (terminal) peloric flower on each plant. Such a flower may not appear in some years, or occasionally more than one may appear, and this seems to be controlled to some extent by the environment, but the capacity for producing a peloric flower is evidently inherited through the seed. In breeding from such a half-race de Vries finally obtained mutations to the full peloric condition, in the fifth and sixth generations of culture. This mutation occurred with a frequency of about 1%, and although highly sterile it probably breeds true. Whether there are any plants which never produce a peloric flower is uncertain.

A similar peloric condition (*Digitalis purpurea monstrosa*) has long been known in foxgloves, in which a single, erect terminal peloric flower occurs on the plant, and opens before the other flowers, which then follow in acropetal succession. The peloric flower frequently also shows an increase in the number of parts. This condition is found by Keeble, Pellew and Jones (1910) to be inherited as a simple Mendelian recessive. The peloric flowers are perfectly fertile with their own pollen, the inheritance being the same through peloric or normal flowers of the plant.

In *Antirrhinum majus*, as in many other plants with zygomorphic flowers, sporadic peloric flowers occasionally occur. There is also a completely peloric race, which Baur (1911) used in his extensive crosses. He concluded that zygomorphy depended upon the presence of two factors P and E. In the absence of E the plant will have only peloric flowers, but plants having E without P (EEpp) produce *both* peloric and normal flowers. This is an interesting case of somatic segregation in the presence of one pair of factors, and presumably there would be no difference in inheritance from the two types of flower on the same plant. If such an EEpp individual is crossed with a fully peloric race (eePP), the F_1 (EePp) bears only normal flowers, while the F_2 gives (1) normal-flowered plants, (2) plants with both normal and peloric flowers, (3) plants with only peloric flowers, in the ratio 9 : 3 : 4. The numbers actually obtained were 70 : 13 : 45, and the departure from expectation (72 : 24 : 32) is explained by the fact that badly nourished plants belonging in class (2) produce only peloric flowers

and hence fall in class (3). Bateson (1902) first pointed out that in reciprocal crosses made by Darwin between normal and peloric snapdragons, the peloric character behaved as a simple Mendelian recessive, giving 90 non-peloric to 37 peloric in F_2. Darwin, however, speaks of two of the 90 plants as being "in an intermediate condition between the peloric and normal state." The exact nature of these intermediate plants is not clear. If they correspond to Baur's class (2), then the actual numbers 88 : 2 : 37 should be compared with an expectation of 72 : 24 : 32 for the ratio 9 : 3 : 4. Hence if the behaviour was the same as Baur describes there would be a large excess of normals to account for, and a corresponding defect of "intermediates."

It is thus obvious that peloria, like doubling, though originating through mutations, behaves differently in different genera.

Other mutations in wild and cultivated plants.

These records are sufficient to show the frequent occurrence of doubles in wild species as parallel mutations, and also of peloria, especially in the Scrophulariaceæ. That they are obviously not in any phylogenetic line of descent however, and are more or less incapable of reproducing themselves, detracts somewhat from their evolutionary interest. We may therefore consider some other types of polymorphism which have arisen in wild species or in cultivation. It has been found practically impossible to draw a line between mutations occurring in controlled cultures and the obviously similar changes which are frequently found wild. We therefore feel justified in extending the mutation conception to these wild forms and varieties.

Linaria alpina, a species of the Alps and Pyrenees, has two varieties, *rosea* and *concolor*, whose genetic relationships have been investigated by Miss Saunders (1912). In the typical *alpina*, which is most common in the Alps, the corolla is blue, with an orange palate, which is partly due to the presence of a viscous orange-yellow fluid in the epidermal cells and the hairs of the beard and partly to the yellowish colour of the cuticle. The var. *rosea*, which is rare and confined to certain stations, is pink with orange palate and behaves as a simple recessive to the type. Var. *concolor* is blue without the orange palate, and this is dominant to the type. Each of the varieties therefore differs from the type by one factor, but it is uncertain which was the original form. In *L. vulgaris*, which is yellow with orange palate, de Vries[1] found on crossing with

[1] Mutationstheorie, II, p. 152.

var. *perlutescens*, which is yellow throughout, that the yellow palate was dominant. Thus yellow palate is dominant in one species and recessive in the other—a quite unexpected result. It is evident that dominance or recessiveness cannot safely be used in determining which is the original or parental type. Even though these are parallel mutations, the alternation in dominance probably depends on an effect of the other specific differences.

In *Digitalis purpurea* several varieties, evidently mutations, have been studied. Saunders (1911), Shull (1912) and others have bred the form called by Chamisso *heptandra* in 1826. The flowers are characterized by dialysis and staminody of the corolla, giving a flower with a petaloid upper lip and seven stamens. But many flowers of a heptandrous plant may show the abnormality in varying degrees, like a wave of reversion advancing up the plant. This variety is a recessive in inheritance.[1] A form *nudicaulis* with smooth stems and leaves less hairy on the upper surface is found by Miss Saunders (1918) to be a simple dominant to the type. Although this condition corresponds to the half-hoary type in stocks, yet in the latter it is due to several factors and behaves as a Mendelian recessive to hoary. This is another example of externally similar characters which are wholly different in their genetic relationships, and it shows that certainty regarding variety relationships can only be attained by actual breeding experiments. *D. purpurea nudicaulis* occurs wild in various parts of England mingled with *pubescens*, the hairy type. The latter is usually more abundant and the indications are that *nudicaulis* has originated from it as a mutation. That a new dominant character can arise by a mutation is known from the case of *Œnothera rubricalyx* among plants or such mutations as bar eye in Drosophila among animals.

From an almost unlimited number of cases of new varieties or forms probably originating as mutations in wild species and often already in process of spreading, we may select a few almost at random.

[1] An exactly parallel mutation has long been known in a North American member of the Ericaceæ, *Kalmia latifolia*. In 1871 Asa Gray (Am. Nat. 4 : 373) described a plant from South Deerfield, Mass. showing dialysis with staminody. It was grown in the Arnold Arboretum and figured by C. S. Sargent (Garden and Forest 2 : 452). It seeds freely, but apparently its inheritance has not been tested. In 1909 Stone (Rhodora 11 : 199) independently reported the same form (var. *polypetala* Nicholson) from the roadside in Leverett near Mt. Toby, and Rehder (Rhodora 12 : 1, 1910) adds a number of varieties, evidently mutational, of this species. Fernald (Rhodora 15 : 151, 1913) records near St. John's, Nfld., a considerable colony of *K. angustifolia* with white corollas (forma *candida*). This form was also found at Sherborn, Mass., and evidently occurs as a sporadic negative mutation which will spread if left to itself.

The ordinary poison ivy, *Rhus toxicodendron* of North America, has fruits glabrous or nearly so. A. H. Moore,[1] records from Bristol, Maine, a form *malacotrichocarpum* with fruits abundantly pilose. *Oxalis stricta*, var. *viridiflora* was described by Hus from St. Louis,[2] differing from the type in having green petals. The same form was afterwards found in plenty by Bartlett[3] near Thomson, Georgia, doubtless arising from an independent mutation. The petals are broader, apparently owing to a change in the shape of the cells, and the presence of chloroplasts may perhaps represent an independent change. *Melica* (*Avena*) *stricta* Michx. has glumes strongly tinged with purple. Forma *albicans* Fernald,[4] the prevailing form on some of the mountains of Maine and Eastern Quebec, has glumes whitish or pale straw-coloured. *Drosera rotundifolia* var. *comosa* is a dwarf variety found by Fernald[5] in a bog at the mouth of the Grand River, Gaspé Co., Quebec. It has a sub-capitate inflorescence of few flowers, petals coloured, and the ovary tending to develop into a rosette of grandular leaves. This dwarf occupied a considerable area in abundance almost to the exclusion of the normal. It is evidently a mutational form able to survive in favourable conditions.

Gaylussacia resinosa, the common huckleberry of America, has black berries without a bloom. Var. *glaucocarpa* Robinson is common in Eastern Connecticut[6] where it occurs in distinct clumps generally associated with the species, from which it differs in having blue glaucous fruits and also in its greater vigor and glaucous leaves. Fernald (1917) describes a colony of *Bidens* by Lake Pocotopaug, Connecticut, which differs from the species *B. connata* of that region in having flat 2-awned achenes like *B. heterodoxa* of Prince Edward Island. He interpretes it as an outlying colony of the northern species, but since its leaves resemble *B. connata* and its var. *petiolata* it more probably represents a parallel mutation.

The American saxifrage, *Tiarella cordifolia* L., extends from New England to Minnesota and southwards. In Maine, New Hampshire and Vermont two forms are found.[7] The plants differ

[1] Rhodora, 11 : 162. 1909.

[2] Rept. Mo. Bot. Garden, 18 : 99, 1907.

[3] Rhodora, 11 : 118, 1909.

[4] Rhodora, 7 ; 244, 1905.

[5] Rhodora, 7 : 8, 1905.

[6] Sheldon, J. L., Rhodora, 4 ; 14, 1902.

[7] Danforth, C. H., 1911. A dimorphism in *Tiarella cordifolia*. Rhodora, 13 : 192-3.

in a single character, having yellow or orange anthers. This is due to a difference in the pollen, which is clear yellowish green in one form and reddish brown in the other. The latter colour is caused by the presence of an orange colouring matter in the cytoplasm, which exudes through the cell wall when the pollen is placed in alcohol or water. Both types of pollen germinate, and plants with the yellow type of pollen appear to be at least twice as numerous as those with the orange pigment. This is of particular interest as showing dimorphism in a gametophytic character.

Leptospermum scoparium is a polymorphic shrubby species occupying vast tracts of New Zealand, with a series of forms also in Tasmania and Australia. It has conspicuous white flowers sometimes stained with pink. In the north of North Island (Cockayne, 1907) a variety is abundant having invariably pale pink flowers, the colour in the petals being confined to the base of the claw. About 1897 a plant was discovered in Otago having petals bright rose colour over their whole surface. This form is known in commerce as *L. Chapmani* and is multiplied by cuttings. Later, on the sandhills 200 miles from where *Chapmani* originated, a plant with rich crimson flowers, was found. It also differed in its more slender, drooping habit, darker foliage, and the flowers were not terminal. From open-pollination a few seedlings like the type were obtained. The evidence indicates that the polymorphism of this species is due to mutation, two of the forms having already established themselves as local varieties.

Coreopsis tinctoria Nutt. is an annual North American Composite, often cultivated and escaped from gardens. It is polymorphic, producing (1) dwarfs, and forms with (2) brown ray florets, (3) tubular ray florets and (4) ligulate disc florets. Raciborski (1908) found in an escaped colony near Lemberg a peculiar type first described by Al. Braun in 1870. It has numerous adventive shoots arising on the internodes and also on the under surface of the leaves along the midrib and was called var. *prolifica*. The seeds from such a plant with brown rays yielded 84 offspring, all but 11 of which showed the adventive shoots. Some of the latter were tall, some short, and a few had yellow rays. Seeds of another (yellow) *prolifica* gave 420, of which all but 16 showed the abnormality. This indicates that the abnormality is probably a recessive, the normals being due to vicinism. Normal plants, however, never gave seedlings with the abnormality, nor could it be produced by wounding or cultivation on rich soil.

Fernald[1] describes *Silene antirrhina*, L. forma *Deaneana* as differing from the type only in the absence of the glutinous band found on some of the internodes in the type. This form is occasional throughout the range of the species, and is constant in the colonies where it occurs. A considerable number of mutations in wild species are given by Hus (1911), and a number of others have been discussed by the writer[2] in their relation to phylogeny. *Betula nana*, L. var. *Michauxii*, of Newfoundland and adjacent portions of Canada,[3] differs from the type chiefly in that the bracts of the pistillate aments are commonly simple and oblong instead of 3-lobed. Similarly *B. alba*, L. var. *elobata*, Fernald, which occurs on Mt. Albert in Gaspé Co., Quebec, differs from the type in the same respect and is evidently a parallel mutation. Near New Boston, New Hampshire, a tree of *B. lenta* was found having deeply serrate leaves,[4] a unit variation. Laciniation of leaves and petals is one of the commonly recorded types of variations in plants.

Rhamnus caroliniana, Walt. is glabrous or glabrate. The var. *mollis*, Fernald[5] differs in having its leaves densely velvety beneath. The pubescent variety occurs in different parts of the range of the species. There is no evidence as to which is the older type. In *Erigeron ramosus* the reverse change has apparently taken place. Var. *septentrionalis*, Fern. and Wieg.[6] differs in having greener foliage, the leaves being sparsely hispidulous or nearly glabrous, instead of cinereous-strigose. The glabrous variety is more northern than the species, occurring in Newfoundland, Eastern Canada, New England and Idaho. This may be because it is better adapted to a cold climate, or merely because it happened to arise in a more northern latitude, but the former seems more probable. A number of species have northern glabrous varieties, but in other species a pubescent variety of a glabrous species is more northern in its distribution. A somewhat different case is found in *Fragaria Virginiana*, var. *terræ-novæ*,[7] which differs from the type in having the pubescence of the petioles and leaves closely appressed. The variety is abundant in Newfoundland, Southern Labrador, and the Gaspé Peninsula where the type is a rarity. It occurs as far

[1] Rhodora, 17 : 96, 1915. Also 12 : 129, 1910.

[2] Gates (1917c).

[3] Fernald, M. L., Rhodora, 15 : 168, 1913.

[4] Sanford, S. N. F., Rhodora, 4, 83, 1902.

[5] Rhodora, 12 : 79, 1910.

[6] Rhodora, 15 : 59, 1913.

[7] Fernald and Wiegand. Rhodora, 13 : 106, 1911.

south as Maine and Vermont, where type and variety sometimes occur together in the same colonies.

The sunflowers of the middle Western States of America are a polymorphic group represented by great numbers of individuals. In 1910 a single mutant of *Helianthus lenticularis* with red instead of yellow rays was found at Boulder, Colorado by Cockerell (1912). It proved to be heterozygous and has since behaved as a simple Mendelian dominant in crosses with other species. In the history of its origin it forms an exact parallel to *Œnothera rubricalyx*. Cockerell (1915) has since studied many elementary forms in the wild species. He quotes from Church the history of the cultivated *H. annuus*, L. which is a gigantic non-branching form. Like maize, its origin in cultivation is only a matter of conjecture. Its seeds furnished the oil supply of pre-Columbian America, and apparently it is a product of Peruvian agriculture. It is very likely a gigantic form of some unknown species perhaps native of Mexico. Its cells should be examined, and their size compared with the cells of other species. Its relation to *H. tuberosus*, the girasole or Jerusalem artichoke, another Indian food plant, is also a matter of interest. In the latter species Cockerell (1919) has described a number of varieties, in cultivation and possible mutations in the shape of tuber, including *multituberculatus*, *fusiformis*, *purpurens* and *purpurellus*.

THE MECHANISM OF ROOT PRESSURE.[1]

By J. H. Priestley.

[With Two Figures in the Text.]

Introduction.

An attempt is made in the following paper to give an explanation of the mechanism of root pressure that shall be in accord with the experimental evidence and with physics and chemistry.

Most of the data presented below are drawn from the work of other investigators, and additional experimental work has only been referred to occasionally where it supplied further evidence for the views advanced.

There is, therefore, little that is new presented below; at the same time it is thought that most of these facts have not been marshalled before as a basis for an explanation of the mechanism of root pressure, and it is hoped that their treatment from this point of view is justified by the satisfactory basis upon which it places this subject.

Arising out of the views stated below, a large amount of experimental work is in progress in this laboratory, and it may be said at once that the work, which it is hoped to publish later, in no way clashes with the theoretical considerations advanced below as to the mechanism of root pressure.

Osmosis is obviously of primary importance in connection with the process by which sap is driven up the xylem from the roots, and, with the aid of Text-fig. 1, an attempt will be made to estimate the significance of osmosis in this process.

In the diagrammatic section of a young root shown in Text-fig. 1, it is permissible to consider all the cells in the series, from the root-hair A to the cell L, bordering upon the xylem vessel, as having cellulose walls, permeable to water and the majority of solutes, and as lined with a layer of living protoplasm, which functions as a semi-permeable membrane. These cells frequently have starch stored within them, and presumably, therefore, sugar is present dissolved in the cell sap. If this sugar is brought down from the leaves by the vascular strands it will tend to be more concentrated in the sap of L, but whatever may be the original concentration in these cells, owing to the entry of water from the

[1] The substance of this paper was communicated to Section K of the British Association, Bournemouth Meeting, September, 1919.

soil solution into the root hair A, a gradient will soon be established in which the concentration of the solutes in the sap of L is greater than in the sap of K, which is greater than in the sap of J, etc.

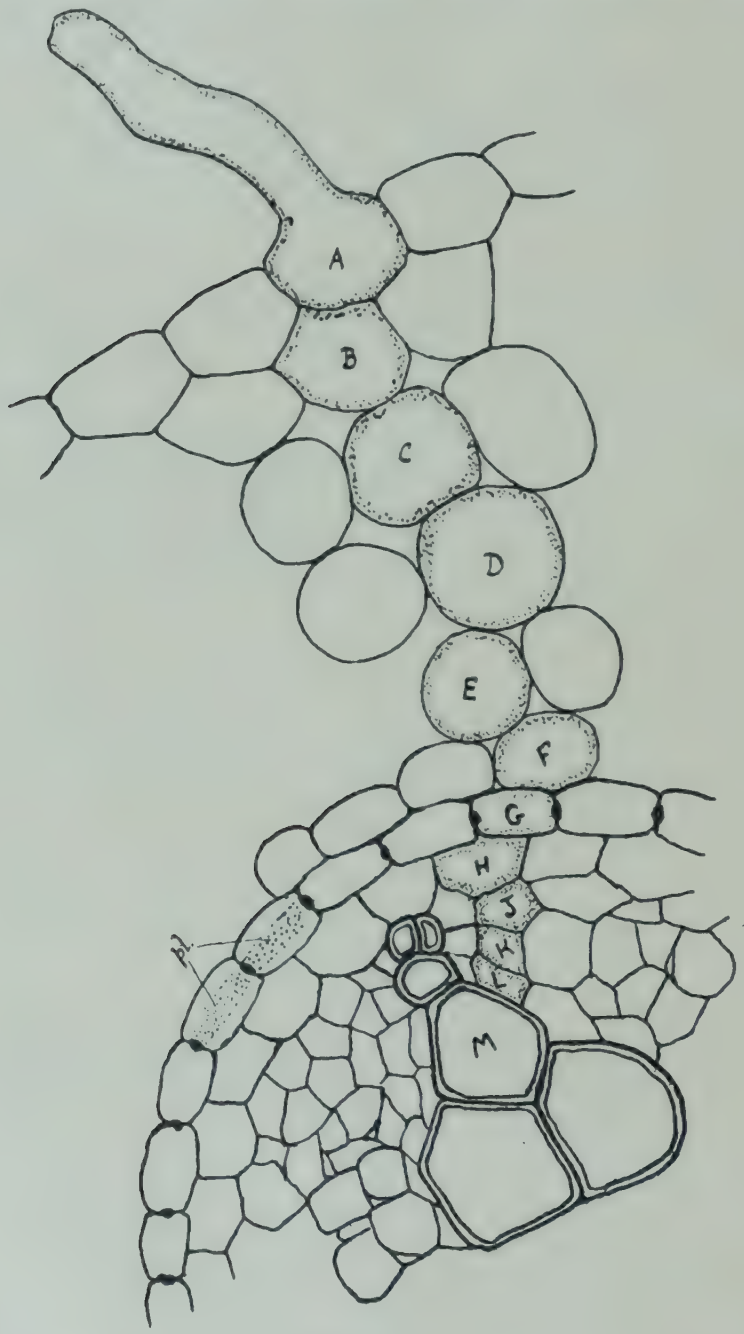

Fig. 1.

As a result of an osmotic gradient of this nature water will be entering the cells of the periphery of the root and passing towards the centre where it will gradually distend the cells of the tightly packed parenchyma within the vascular cylinder.

We can then understand the passage inwards of the water from the surface of the root to cells in the position of L, Text-fig. 1, but the further passage of the water into the cavity of the xylem vessel seems at first sight to present a difficulty. The cellulose wall of L is completely lined within by the usual semi-permeable layer of protoplasm, whilst M has no such lining. Under these conditions, unless the sap within M contains a sufficient concentration of solutes to be in osmotic equilibrium with the cell sap of L, water will apparently be withdrawn from M to L by osmosis. But if the cell sap of L is under sufficient pressure, the sap may remain in equilibrium with a more dilute solution in M, which, protected by its rigid lignified wall, is not under the same pressure. Gelston Atkins (1, loc. cit. p. 201) has, in reality, invoked this explanation when suggesting that the ascent of water in the xylem of the root may be explained as an osmotic phenomenon, acting from the dilute sugar solution in the xylem to the soil solution outside, through a mass of living cells, *treated as one semi-permeable membrane.*

The parenchyma within the endodermis, *e.g.*, the cells H, J, K, L, are confined within an endodermis, the extensibility of which is limited, the radial walls of the cells being clamped by lignified thickenings; and frequently the other walls of the endodermal cells are also greatly strengthened.

No air spaces are present between the cells, and the walls of the xylem vessel are rigid. Between endodermis and xylem vessel, the cells then are practically unable to expand, and under these conditions it is physically possible to have the internal hydrostatic pressure, within cells in the position of L, so high that water may be forced into M, although the solution in M has a lower osmotic pressure than the cell sap of L.

The function of the endodermis in this process will now be considered more closely, but it must first be pointed out that the hydrostatic pressure exhibited by the cells from H to L will not alone explain the continuous rise of water in the xylem vessel M, although it would explain the sap in L remaining in equilibrium with a less concentrated solution in M. M would have to retain a very appreciable osmotic pressure, and, as M contains no living protoplasmic contents, the only conditions under which this would seem possible, would be under circumstances which would permit of a constant supply of solutes to M from the adjacent cells. The phenomena investigated by Lepeschkin in the excretion of water by hydathodes seem to throw light upon this question.

To understand the possible mechanism by which the water in L can be continually supplied to M, it will therefore be necessary to discuss two questions, (1) the significance of the endodermis, (2) the excretion of water by superficial hydathodes.

The endodermis. As the water passes inwards from the cortex of the root the endodermis is the first continuous, unbroken layer of cells encountered (a somewhat similar layer may be present near the exterior of the root in the form of an exodermis and possibly its function may be interpreted upon somewhat similar lines to those adopted in the subsequent discussion upon the functions of the endodermis).

The continuous layer of endodermis in a young and functional root encloses a core of tissue in which parenchyma, sieve tubes and xylem vessels are tightly packed without intervening air-spaces.

A very characteristic feature of the endodermis is the thickening of the radial walls, which usually have the same staining reactions as the lignified xylem walls, but this radial thickening is not itself merely lignified. On the contrary, there is very considerable evidence (Haberlandt, 6, loc. cit. pp. 368, et seq.) that this radial thickening is suberised and impermeable to water. The same thickening of the radial wall is visible in longitudinal sections of the root and it is easy to establish that this impermeable strip is continuous all round the radial transverse and radial longitudinal walls of the cell.

This means that, as the water passes from the cortex of the root into the central core through the cylinder of endodermis, it cannot follow a path across the endodermis such that it remains always in the wall, it must enter the protoplasm.

De Rufz de Lavison (4, 1911) has brought out this point very clearly. He has shown that even when the cells are vigorously plasmolysed, the protoplasm is not withdrawn from the suberised strip, the plasmolysed protoplast always taking the form shown at 'pl' in Text-fig. 1.

De Rufz de Lavison (3, 1910 and 4, 1911) has also shown that solutes in the water surrounding the root, if unable to penetrate the protoplasm, can diffuse into the root as far as the endodermis, diffusing inwards by the walls, but they are then completely stopped at the endodermis. Similarly if the root tips are cut across, and the cut ends dipped into water so that this is then drawn up through the xylem by the ascending current due to transpiration from the leaves, if the ascending water currents contain a substance, incapable of penetrating the protoplasm, but whose passage through

the walls can be followed by its colour or by subsequent staining reactions, then this substance will be traced diffusing outwards as far as the endodermis and no further. These experiments of De Rufz de Lavison seem very conclusive, and quite similar results have been obtained by the writer, but are not described in detail as De Lavison's papers are readily accessible.

De Lavison (3, loc. cit. 1910), likewise Haberlandt (6, loc. cit. pp. 371, 372) refers to experimental work of de Vries (10, 1886) not accessible in the original to the present writer. In these experiments de Vries apparently found that if he forced water into the root from the surface of the cut stem it was impossible to obtain a leakage of this water from the root unless the endodermis was injured. Presumably a pressure was never used which exceeded in magnitude the opposing osmotic pressure retaining the water within the protoplasts of the endodermal cells.

The above facts taken in conjunction lead then to the conclusion that water, in passing through the endodermal cylinder, must pass through the protoplasts. As the considerations studied previously show that these protoplasts find themselves linked in a series of cells in which the osmotic gradient rises towards the inside, this is tantamount to saying that under normal conditions the passage of water through the endodermis is completely controlled by osmotic phenomena, and is always taking place in an inward direction. Before considering the further bearing of these facts we will discuss the significance of some modern work on the excretion by hydathodes.

(2) *Excretion by hydathodes.* The hydathode is one special case, dealt with by Lepeschkin (8, 1906) in his study of the excretion of water by plants.

For details reference must be made to the original papers; for present purposes, it is sufficient to cite the facts as to the excretion of water by the multicellular hair of *Phaseolus multiflorus.* (Fig. 2.)

On the basis of his experimental results with the young sporangiophore of Pilobolus, Lepeschkin explains the continuous excretion of water from the two top cells of this hair by the assumption of a different semi-permeability of the protoplasmic layer on the upper, as compared with lower, side of the cell.

If this protoplasmic layer is more permeable on the upper side, then before the internal hydrostatic pressure arrives at the level that it is possible to obtain through the entry of water at the lower side of the cell, water *and certain solutes* will be passing out of the cell at the top on to the upper surface. This excretion of water

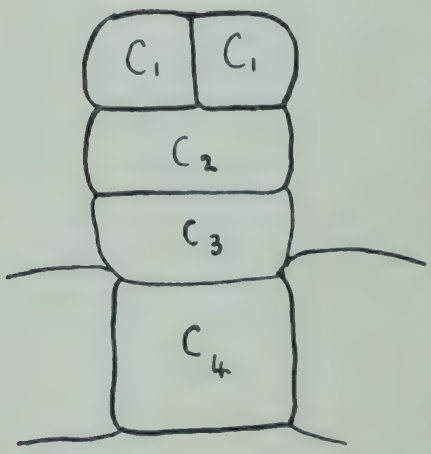

Fig. 2. Diagram of multicellular hydathode of *Phaseolus multiflorus*.

Text-fig. 2 represents sufficiently the conditions prevailing in one of these excretory hairs, where we have a series of cells with permeable cellulose walls, lined by semi-permeable protoplasmic membranes, and with internal osmotic concentrations such that C4 is less than C3 is less than C2 is less than C1, but C4 is greater than the osmotic concentrations of the epidermal and mesophyll cells surrounding it.[1]

and solutes will continue so long as there are sufficient solutes to maintain C1 higher than C2 and also high enough to generate a hydrostatic pressure sufficient to force water and solutes through the upper surface of the cell. It is important to notice that in a hydathode functioning in this manner (compare the hydathodes of *Colocasia anti-quorum*, see p. 198) the excretion, if arising from the causes explained above, will never be pure water. In fact it is difficult to see how the excretion of pure water under such conditions could be harmonised with thermodynamics; water would be moved and work done, apparently without energy being expended, as the osmotic concentration within the cell would then remain unaltered.

The solutes in the excretion were usually inorganic. Lepeschkin found for example, the following percentages of inorganic ash in the excretions from superficial cells of the plants named:—*Phaseolus* 0·4%, *Abutilon* 0·5%, *Nicotiana* 0·1%, *Polypodium* 0·2%, *Camellia* 0·5%, *Lathyrus* 0·5%. He found organic substances in the excretions in the following cases;—*Lathyrus odoratus* (alkali salts of organic acids); *Vicia sativa* and *Polypodium aureum* (glucose). The excretion was alkaline, except in the case of *Lathyrus*. $CaHCO_3$ was usually present in a relatively large proportion amongst the inorganic salts.

Returning to our present problem of root pressure, it will readily be seen how the data cited above enable us to fashion a hypothesis to overcome our difficulty of the passage of water from the cells (as L, Text-fig. 1) bordering on the xylem vessels, into the xylem vessels.

[1] Bayliss (2 loc. cit. p. 163) describes the osmotic concentration in these hairs as decreasing from base to apex, but undoubtedly he has quoted Lepeschkin incorrectly.

Throughout all the mass of parenchyma, packed between the rigid xylem tubes of the centre and the relatively rigid (frequently strongly lignified) outer cylinder of endodermis, a strong hydrostatic pressure is developing owing to the entrance of water, governed by the existing osmotic gradient. Cells such as G (Text-fig. 1) are in the position of the basal cells of the hydathode (with concentration C4, Text-fig. 2), cells such as L (Text-fig. 1) are equivalent to the apical cells of highest osmotic concentration (C_1, Text-fig. 2). If then, we make the same assumption as Lepeschkin, and assume that the protoplasmic membrane of L, as it abuts upon the xylem, is of relatively greater permeability than the protoplasmic layer of L where it abuts on other parenchymatous cells,[1] then we have the conditions existing for an excretion of water, *plus solutes*, into the xylem vessel so long as the osmotic pressure in L is greater than the osmotic pressure in K, and so long as the hydrostatic pressure generated within the core of tissue within the endodermis is strong enough to force water and solutes into the xylem vessel from L.

When this stream of water and solutes enters the xylem vessel M, the only direction in which it is free to move is upwards in the cavity of the vessel. It is true it may leak through permeable cellulose walls, around the protoplasts, back as far as the endodermis, but at the endodermis it meets the barrier of the suberised region and cannot leak outwards any further (see page 4).

At this point it is necessary to refer to a few simple experiments which support the hypothesis outlined in the preceding paragraphs.

It would appear at first sight that even if water may not leak outwards from the xylem vessel to the surface because of the suberised walls of the endodermis, a slight leak might occur near the root tip where the endodermal cylinder is not yet differentiated. Such a leak would probably in any case be a minor factor, as the *walls* of the cells in the apical region, through which alone this leakage could take place, are very thin and the outward diffusion under the existing pressure through their total cross section would be small. But as the result of a number of experiments in this laboratory with various readily penetrating dyes, it is suggested that even this amount of leakage probably does not take place. As stated previously, de Rufz de Lavison's observations that such

[1] For this difference in permeability good structural cause may well exist. The ectoplasm in one case will be supported by a similar layer opposed to it, to which it is attached by protoplasmic connexions, in the other case the ectoplasm faces a "dead" lignified layer.

a dye, if it cannot penetrate the protoplasm, does not penetrate through the walls further inwards than the endodermis have been confirmed. In the course of these experiments it was noted that at the root tip the penetration inwards via the walls was even less marked. To obtain the result it is necessary to experiment with roots that have been previously grown in water: otherwise, when the roots are transferred to the dye solution toxic conditions are invariably produced and the dye penetrates right through the tip, freely entering the dead cells.

These observations have been made on willow roots and onion roots, using various dyes chosen for their penetrability on the basis of the valuable data given by Ruhland (9, 1912). Good results have been obtained with light green FS, orange G, neutral red and malachite green.

These dyes penetrate cellulose walls readily and in some cases can penetrate the living protoplasm. Their inability to penetrate at the root tip suggests, therefore, that the cell walls in the neighbourhood of the apex have the properties of protoplasm rather than of dead cellulose walls, at any rate with regard to diffusion. By the use of such dyes it is also possible to obtain ready confirmation of the greater permeability of the apical cells of the hydathodes of *Phaseolus vulgaris*. If a leaf of this plant be dipped in dilute (0·05%) aqueous neutral red, for a few hours, and then a section of the leaf is examined in water, the plasma of the apical cells of the hydathode will be found to be deeply stained, but the lower cells of the stalk will not be stained even after 24 hours' immersion.

That some of the cells within the endodermis likewise have a greater permeability relatively to the endodermal cells, has been illustrated by similar experiments, so that these cells correspond in this respect to the apical cells of the hydathode and the endodermal cells to the basal cells. In these experiments young plants are taken and their root tips cut across under water and the roots then placed in aqueous solutions of various dyes (usually 0·1%). Best results have been obtained with acid green, malachite green, neutral red, and light green FS. But various seedlings may be used and probably the exact combination of seedling and dye for best results varies with different external conditions. The solution of the dye is then drawn up the xylem and the water previously inside the vessels is drawn up to the leaves to replace that lost by transpiration.

If a section is cut across the root some 24 hours later, the walls of the xylem will be found to be stained, and possibly the dye will have diffused via the walls as far as the endodermis, any patches of thick walled sclerenchyma within the endodermis being thus quite likely to show their walls well stained. But the protoplasts within the cells will still be quite colourless, except for some cells close to the xylem, but not always immediately adjacent. Frequently these cells form a group lying between protoxylem and endodermis. These cells will stain deeply and show up most conspicuously, owing to the fact that the dye has in many cases penetrated them and accumulated within them. The effect has been particularly well seen in this laboratory, using acid green and seedlings of *Vicia Faba*.

It is submitted then that the hypothesis outlined above, based on the work of other investigators and supported by a small amount of new experimental evidence, provides an adequate basis for the interpretation of the phenomenon of root pressure. It is not pretended, however, that the hypothesis is free from difficulties and one or two of these will now be briefly considered.

One outstanding difficulty in the case of a hydathode which functions for some considerable period, is accentuated in the case of the root where a very considerable stream of water may pass upwards. It is difficult to understand how the necessary solutes can be provided in sufficient quantity to permit of the constant leakage of the solute across the inner membrane of cells such as L. (Text-fig. I).

From Lepeschkin's work, such solutes might be either organic or inorganic. It is suggested tentatively that in the root they are organic, and either sugars, or, more probably, organic acids derived from the breaking down of sugars. Of these sugars probably a constant supply is available from hydrolysis of the stored starch or from the sugars arriving by translocation from the leaf. In favour of the view that the solute is a sugar may be quoted the data given by Gelston Atkins (1, loc. cit. Chap. XI) as to the presence of sugar in the sap rising in the xylem, and the interesting data as to the permeability of blood corpuscles to glucose, discussed by Bayliss (2, loc. cit. pp. 126 and 127) which leads him to the conclusion that "The facts suggest the possibility that the normal semi-permeability of the membrane to glucose is connected with a particular difference of concentration on the two sides, but that the actual value of this difference may be changed by other influences."

This conclusion of Bayliss leads to another consideration it may be well to keep in mind. If the permeability of a protoplasmic membrane to glucose is a function of the difference of concentration on the two sides of the membrane, then the accumulation of sugar within L, or the dilution of this sugar by entrance of water, might be factors leading to a change in the permeability of the protoplasmic membrane on the side bordering on the xylem vessel, and such a change might have the result of rendering the membrane on this side *temporarily* permeable to sugar. In other words, instead of the constant excretion of water, noted by Lepeschkin in the hydathodes under observation, we may here be dealing with an intermittent phenomenon in which changes in permeability follow upon the changes in concentration within the protoplasts bordering upon the xylem, the original permeability, or lack of permeability, being restored as these concentrations readjust themselves by temporary discharge of water and solute into the xylem stream. This process, intermittent in the individual cell, would appear as a continuous process in the phenomenon of root pressure, where the final result is the sum of the activities of many thousands of cells in different phases of activity.

Returning from this digression to the problem as to the constant provision of the solute which passes out with the water into the xylem vessel, the hypothesis that this solute is an organic acid derived from sugar has much attractiveness. As pointed out by Bayliss (2, loc. cit. p. 165), such chemical changes permit of rapid increase in the osmotic concentration, one molecule of glucose giving rise to several molecules of acid. Futhermore, the experimental data already accumulated (see for instance Hind 7, 1914, p. 229, et. seq.) show that protoplasm is relatively rapidly permeable by organic acids under some conditions, though the facts of translocation drive us to assume a similar permeability for sugars under certain unknown conditions.

Another difficulty is the apparent contradiction between the assumption that solutes enter the xylem vessel with the water of the root pressure stream, and the facts recorded by Flood (5, 1919) in the case of the excretion from the leaf tips of *Colocasia antiquorum*. This very vigorous excretion has been shown to be due to the activity of the roots in pumping water up, and, during its upward passage until its exit at the tip, the water passes through no filtration mechanism whatever. But the water excreted is practically free from impurities. In that case what becomes of the

assumption that solutes must enter the xylem vessel from the secreting cells in the root?

The assumption and the factor are probably reconcilable, on the grounds that after excretion and during the subsequent upward passage in the xylem the ascending stream is always in contact through the xylem walls with the surrounding protoplasts. Under these circumstances, physical adsorption on the surfaces limiting the stream may well be followed by physiological absorption, whether the solutes in the ascending stream are organic or inorganic, sugars or acids.

This suggestion must probably appear in any theory of root pressure, because the fundamental tenets of thermodynamics seem difficult to reconcile with any other assumption than the original excretion of solutes with the water into the xylem vessel.

It is not claimed that this discussion is exhaustive, but it is submitted that the account of the mechanism of root pressure given above fairly states the difficulties and provides, with the minimum of assumption, a hypothesis, founded chiefly on observation and experiment, that is adequate to account for the facts.

This hypothesis should be of interest because on the one hand it suggests the revision of anatomical data with reference to the endodermis to see if they will permit this interpretation of its function and on the other it points the way to a series of physiological investigations which may throw further light on the phenomena of permeability.

It is hoped to give a more detailed account later of the experimental work arising out of the views stated above, and with such an account other names would be associated. In connexion with the experimental work briefly touched upon above, I have to acknowledge the help of Miss D. Armstead, Research Assistant in the Department, and of Miss Tupper Carey. I should also like to express my great obligation to Dr. S. A. Shorter, for his patient assistance in helping me to struggle towards enlightenment on the physical side of the problem.

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METHODS AND SIGNIFICANT RELATIONS IN THE QUANTITATIVE ANALYSIS OF PLANT GROWTH.

By C. West, G. E. Briggs, and F. Kidd.

THE present authors are conducting a comprehensive study of the growth of *Helianthus* and are publishing (4) the results they have obtained from an analysis of the huge mass of data presented in the literature nearly half a century ago by Kreusler and his co-workers (7). It has been brought home to them very clearly in the course of this work that the previous attempts to express growth by some simplified formula are based upon a superficial similarity or upon wrong assumptions.[1] The effect of such generalisations has been to give an air of finality and to divert attention from the possibilities of deeper analysis. It is the formulation of methods for such an analysis that appears to us most urgent at present, and we have thought that it would be of interest to put forward at this stage the data and relations that seem to us significant.

The Unit of Measure.

In considering the problem of plant growth the plant physiologist is faced with the question as to what unit of measure he shall adopt. From whatever point of view the growth of a plant

[1] For a more detailed consideration and criticism of these formulæ the reader is referred to (4).

as an organism be considered, growth appears most broadly speaking as a process of increment in dry-weight. Accordingly, in line with the practice of previous investigators in this branch of plant physiology increase in dry-weight may be adopted as the best measure of growth.

The Study of Growth Rates as opposed to the Study of Final Yields.

Until recently the idea of rates as applied to the growth of the plant as a whole has been only vaguely conceived. Investigators, especially those working along economic lines, have been concerned mainly with the final yields. A study of plant growth from the outlook of rate is, however, more fundamental in so far that it aims at disentangling the details of the mechanism of growth and at a precise knowledge of the factors limiting growth throughout its course.

A solution of the problems of growth may be regarded primarily as the precise determination and evaluation of those factors, internal and external, which control the *rate* of the plant's increase in dry-weight from time to time throughout its life-cycle. Secondarily, after these factors are known and their values expressed in appropriate units, we may be in a position to state constants for the growth-rate of particular plants applicable to the whole life-cycle, and such constants will not only be of use from the economic point of view in comparing plants, but also will have physiological significance.

A rate is the amount of change per unit time. The actual rate of growth is the increase in dry-weight per unit time and depends upon various external factors and upon what we may call the amount of the "growing material."[1]

Growth Rate expressed per Unit of Dry Weight.

It is clear that if we could determine the unit of "growing material" it would be possible to express the rate of growth per unit of "growing material," and we should then be in a position to evaluate the various external factors and to determine specific plant constants. Under constant external conditions the rate so expressed would remain constant for a given plant, and changes in rate observed would be related to changes in external factors when these factors are limiting the rate. Let us take the simple case of a population of unicellular organisms growing in a medium the composition of which, together with other environmental factors, is constant. In such a case the actual rate of growth, as

[1] The term "amount of growing material" is equivalent to the 'active mass' of the reactant in a chemical reaction.

measured by the size of the population or its dry-weight, is found to increase exponentially with time, but the rate per unit of population or per unit of dry-weight is constant throughout (14). We may, therefore, legitimately take the dry-weight at any moment as a measure of the material actually engaged in growth at that moment and proceed at once to the determination of a growth constant.

In this simple case the method of expressing the rate of growth is physiologically sound in so far as the rate remains constant under constant conditions, and changes in rate would be expressions of changes in environment. The soundness of the method depends upon the fact that all the material is equally active in forming new growth by cell-division and by assimilation of new material, and hence the dry-weight of any time is a measure of the material responsible for dry-weight increment and growth.[1]

In the higher plants the state of affairs is more complex. The material of the plant is not all equally active in forming new growth by cell-division and by assimilation, and moreover we do not know that the relation of the amount of material actually engaged in growth to the total material (dry-weight) is constant: in fact the evidence from morphological considerations and from analyses of growth data carried out by the present writers (4) is that the relation undergoes a definite type of variation. Consequently, in relating growth to dry-weight in the higher plants we are not relating growth to the amount of actual "growing material." The growth-rate expressed per unit of dry-weight does not remain constant under constant external conditions and we cannot therefore, on this basis alone, determine constants for the plant, nor can we evaluate the effect of environmental factors.

Previous Attempts to evaluate Constants for Plant Growth.

In practically all previous attempts to evaluate constants for plant growth the rate, *i.e.*, increase in dry-weight per unit time, has been expressed per unit of dry-weight. The formula $\frac{dx}{dt}=Kx\ (A-x)$, or in its integrated form $\log\frac{A-x}{x}=K\ (t-t')$, which is the autocatalytic formula put forward by Robertson (12 & 13) as expressing the growth of an organism, and which Reed (8 & 9) and Rippel (10 & 11) apply to the growth of the plant organism, involves the assumption that since K is constant,[2] x, the dry-weight, is a measure of the "grow-

[1] The result is actually a statistical one, assimilation preceding cell-division in the individual, but at any moment both processes are going on when the population as a whole is considered.

[2] Reed goes as far as to assume that K is a constant apart from A.

ing material" and also that the rate per unit of "growing material" decreases throughout the life cycle owing to the disappearance of a catalyst as growth proceeds. Such a formula, which fits the facts only approximately and explains the falling off in rate per unit dry-weight as being due to the disappearance of a catalyst, obviously does not help us much in an analysis of plant growth, and we agree with Enriques (5) that the similarity between an autocatalytic reaction and the growth of a plant is a purely superficial one, the falling off in rate per unit dry-weight being due rather to increasing differentation into productive and non-productive tissues.

The formula $\frac{dW}{dt}=rW$, or in its integrated form $W=W_0e^{rt}$, originally put forward by V. H. Blackman (1) with the idea that it was an important physiological constant, involves the assumption that dry-weight (W) is a measure of "growing material." It has been shown that the rate per unit dry-weight, r, is not a constant (3 & 6).

Suggested Procedure in the Study of Growth Rate.

Before we can determine constants for a plant which have any physiological significance and which are comparable with physico-chemical constants we require a much more detailed analysis of the growth throughout the whole life-cycle. To this end we consider that the best procedure is to calculate the rates in relation to various units of the plant from data collected at frequent intervals. In this way we obtain a number of parallel records of rates throughout the life-cycle. By a careful comparison of these with each other and with the records of environmental factors we may hope to disentangle the problems of plant growth and proceed to the evaluation of constants. More in detail our technique and terminology are as follows:—

(1). *Primary Data.* Measurements of dry-weight and leaf-area at intervals of a week or less accompanied by measurements of respiration, assimilation, transpiration and chemical analysis of the plant tissue, and continuous records of the various environmental factors likely to affect growth. In order that these data when collected may be of real value it is necessary to adopt a sound statistical procedure, *e.g.*, utilisation of material as uniform as possible, large samples and calculation of probable errors.

(2). *Significant Secondary Relations.* The presentation of the results so obtained through the complete life-cycle in four series of numbers which can, if desired, be put in the form of graphs—"*Relative Growth Rate*," "*Leaf Area Ratio*," "*Unit Leaf Rate*" and "*Relative Leaf Growth Rate.*"

The *Relative Growth Rate*, R, is the weekly percentage rate at which the dry-weight increases. It may be assumed for purposes of calculation that the increase from week to week takes place exponentially, R being the exponent, or that it takes place linearly. Both are approximations. As to the relative merits of the two different methods the reader is referred to (4). If R be the *Relative Growth Rate* and W the dry weight then $\frac{dW}{dt}=\frac{RW}{100}$. This formula expresses the relation between R and W assuming the increase takes place exponentially and when integrated the equation becomes $\log_e W_2 - \log_e W_1 = \frac{R}{100}$, where W_2 is the dry-weight at the end of the week, W_1 the dry-weight at the beginning of the week and e the base of the natural logarithms. If it is assumed that the increase is linear $\frac{R}{100}=\frac{W_2-W_1}{W_1}$.

By *Leaf Area Ratio*, A, is meant the ratio of leaf-area to dry-weight, that is $\frac{L}{W}$. For simplicity $\frac{\frac{L_1+L_2}{2}}{W_1}$ is used when making calculations on the linear basis, L_1 being the leaf-area at the beginning of the week and L_2 at the end of the week.

By *Unit Leaf Rate*, E, is meant the weekly rate of increase in dry-weight per *Unit Leaf Area*.[1] Then $\frac{dW}{dt}=EL$, and if the exponential basis be adopted for both leaf-area and dry-weight increase, then $E=(\log_e L_2 - \log_e L_1)\frac{W_2-W_1}{L_2-L_1}$. On the linear basis for leaf-area $E=\frac{W_2-W_1}{\frac{L_1+L_2}{2}}$, that is, the weekly increase in dry weight divided by the Average Leaf Area.

Relative Leaf Growth Rate, R_L, is analogous to Relative Growth Rate and $\frac{R_L}{100}=\log_e L_2 - \log_e L_1$, or $\frac{L_2-L_1}{L_1}$ according to whether the calculations assume an increase on the exponential or on the linear basis.

An inspection of the above definitions and formulæ will show that whichever formal conception as to the mode of increase of dry-weight and leaf-area be adopted the Relative Growth Rate is merely the product of the Leaf Area Ratio and the Unit Leaf

[1] Cf. Weber's "Specifische Assimilationsenergie" (15).

Rate multiplied by 100. This will be made clear by the following. On the exponential basis $R=\frac{100\ \frac{dW}{dt}}{W}$, $A=\frac{L}{W}$ and $E=\frac{\frac{dW}{dt}}{L}$ and hence R=100A.E. On the simple interest basis it will be seen that the same relationship holds. None of the above formulæ involve the assumption that R, R_L, A or E are constant throughout the life-cycle.

An examination of data shows that in the early part of the plant growth the increment of dry-weight and of leaf-area is more or less exponential, whilst later it approaches to being linear. Thus in order that the calculated rates may approximate more closely to accuracy, especially in the case of the Unit Leaf Rate, the exponential basis should be adopted in the early period whilst in the later period it makes little difference in the calculated rate which basis of calculation be adopted. The importance of obtaining values for Unit Leaf Rate which approach closely to accuracy is that these values may be compared with values of assimilation determined by gasometric and half-leaf methods.

Our reason for adopting Unit Leaf Rate as a significant relation in the analysis of plant growth is that we have at our disposal a certain amount of definite knowledge with regard to the effect of environmental factors upon assimilation. By making the necessary allowances for variations in environmental factors we can determine to what extent assimilation controls growth and to what extent it is controlled by growth.

Another problem which can be attacked by the above method is as to how far differences in *Relative Growth Rate* of different plants are due to differences in *Unit Leaf Rate* and how far to differences in *Leaf Area Ratio*. This problem is now under experimental investigation by the authors.

In the case of maize the ratio of productive to total weight is not constant but the *Relative Growth Rate* and *Leaf Area Ratio* undergo similar and simultaneous variations, thus suggesting that *Unit Leaf Rate* is roughly constant throughout the main parts of the plant's life-cycle, and that, considering the growth of a plant as analogous to money accumulating interest, the leaf-area is a better measure of capital than is the dry-weight.

The above suggestions are to be considered simply as proposals for formal methods of assembling secondary data on what appear to be the most profitable lines as a result of the closest inspection possible at present. It is to be emphasised that

the relations it is proposed to record at weekly intervals throughout the life of a plant do not involve any general presumptions as to the factors controlling growth as a whole, such, for example, as the presumption that growth is controlled by assimilation or that growth is controlled by root absorption. Our attitude is that general conclusions should be postponed until sufficient secondary data, based on sound primary data, have been carefully analysed. From the primary data mentioned above other secondary data in addition to those proposed by us can obviously be obtained, and as analysis proceeds it is possible that some of such further relations may be found to be significant in finally arriving at conclusions with regard to the various factors controlling growth.

The quantitative analysis of plant growth week by week by some such method as that outlined has not been carried out before, and we have been influenced in putting forward our tentative suggestions by the hope that they will stimulate and be of use in further research. It is obvious that it would be a distinct advantage if various workers on this problem would make use of the same general methods or at least present their results not only in graphical form but also by giving the actual figures obtained. It is much to be regretted that such a contribution to the subject as that of Brenchley (3) is devoid of any primary data whatever concerning the plants themselves.

Botany School, Cambridge. *June, 1920.*

NOTE.

In reply to a suggestion put forward by us in the previous number of this journal (6) to the effect that from an economic point of view the "substanzquotient" is preferable to the "efficiency index" in that it only states the ratio of final weight to seed weight divided by time and makes no assumption as to the rate of addition of dry material, Professor V. H. Blackman (2, p. 99) states that "a formula in which final weight is divided by seed weight and by time implies that there is a linear relation between time and weight." This would have been the case if we had said that the "substanzquotient" was a constant, but we stressed the point that the "substanzquotient" varied with time and hence had no physiological significance.

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PRELIMINARY NOTES ON ADDITIONAL EVIDENCE FOR THE HYDRION DIFFERENTIATION THEORY OF GEOTROPISM.

I.—On the Reversal of Geotropic Curvature in the Stem.

By J. Small and M. W. Rea.

SINCE the publication by one of us of a theory of geotropism supported by certain experiments (2) some considerable amount of additional evidence in favour of this theory has been obtained. The details of this evidence will not be published for some time, and therefore this preliminary account is being given.

The theory of the experiments is, briefly, that the differentiation in hydrion concentration in stem and root is caused by the comparatively slow escape of the CO_2 of respiration from the root, which thus becomes relatively acid; and the rapid elimination of that CO_2 from the stem and leaves either by diffusion through the stomata or by its utilisation in photosynthesis or by both these methods. The shoot therefore becomes relatively alkaline and the hydrion differentiation is in this way connected with the normal metabolism of the plant.

From this hypothesis it follows that when shoots are placed horizontally in the dark they may cease to react or may react in the reverse direction to the normal under geotropic stimulation. If these shoots are coated with vaseline the CO_2 of respiration should accumulate within and the geotropic response should be reversed.

Shoots of a number of very different plants have been treated in this way, *i.e.* coated with vaseline and placed horizontally in the dark. Most of the shoots so treated showed downward curvatures, while shoots left in the dark unvaselined in a number of cases showed upward curvatures and in others showed either no curvature or downward curvatures. The plants which showed reversed curvature include maize, *Pelargonium*, *Cerastium*, sycamore seedlings, *Myosotis* inflorescence, *Antirrhinum* seedlings, groundsel and *Anthemis*. No upward curvature or positive downward curvature in the dark has been observed in unvaselined specimens of maize, *Stellaria media* and sycamore seedlings. Photographic records of these experiments have been kept and we intend to give a detailed account when the problem of the CO_2 balance has been more thoroughly investigated. One point, however, should be noted. If the plants are placed horizontally in the dark immediately after

being vaselined they curve upwards as a rule. They must be placed vertically in the dark for two to seven days, to allow the CO_2 to accumulate, if downward curvature is to be demonstrated. In several cases recovery from downward curvature to upward curvature was obtained by placing the plants in the light, to enable them to remove the CO_2 by photosynthesis. The treatment with vaseline and darkness also inhibits the growth of the stem (cp. 1).

A practical application of the phenomenon which has just been described occurs in the "earthing-up" of potatoes; the "earthing-up" increases the amount of CO_2 in and around the lower stem branches with the result that they grow down into the soil and ultimately produce tubers, which may be regarded as physiological malformations due to the disturbance of the normal condition of the protoplasm. This explanation of the production of potato tubers may be extended to include the experience by farmers in the north of a loss in the potato crop, instead of a gain as with barley, when the plants are treated with high tension currents. To put the matter briefly—whereas the positivity of the high tension currents induces a negative charge in the already negatively polarised sub-aerial parts, that same positivity decreases the polarisation in the already positively polarised subterranean parts with consequent increase of permeability, loss of turgor, loss of growing power and decrease in tuber-production.

II.—On the Angle of Balance in Roots, Stems and Leaves.

By J. Small and M. J. Lynn.

In the above mentioned paper (2, p. 58, Fig. 5) an explanation, based upon the new theory of geotropism, is given of the orientation of secondary roots and stem branches. Certain deductions from that explanation are obvious. (1.) Provided that the distance of the point of junction from the tip of the main axis remains constant, the angle of balance will increase with the growth in length of the of the lateral organ, because the strength of the action current in it *at the point of junction* will decrease, and therefore a greater angle, giving a larger action current, will be required to balance the leak of the normal polarity current from the main axis. Since it has been shown (3, 4, 5) that the strength of the response (or action current) varies as the sine of the angle, it follows that when the angle of balance is plotted against the length of the lateral organ, the graph should be a sine curve. (2.) Provided that the length of the lateral organ remains constant, the angle of balance will

decrease with the growth in length of the main axis on the apical side of the point of junction, because the strength of the leak of the normal polarity current *at the point of junction* will decrease, and therefore a smaller angle, giving a smaller action current, will be required to balance that leak. These deductions are made with the additional hypotheses that the meristems of the lateral organs are more or less the same size in all the secondary roots *or* stem branches *or* leaves of the same species, and that the apical meristems of the main roots *or* stems are likewise constant within limits.

The angle of the lateral organ with the main axis would then vary directly as the length of the lateral and inversely as the distance of the point of junction from the apex of the main axis. If L be the length and D the distance, then the fraction L/D should vary as the sine of the angle.

Measurements have accordingly been made of the root-system of the pea, of the branch systems of the privet, cherry-laurel, *Rumex*, yellow cress and *Equisetum*, and of the leaves of *Pelargonium*, *Chrysanthemum*, *Rumex*, hazel and mint. The branches and roots have yielded curves which are similar within ten degrees either way to the sine curves for the angles found. The leaves have yielded similar curves which are, however, different in direction although not in kind. Superficial observations of many other herbs, shrubs and trees readily show that the same relations hold in them for both stem and leaf angles and lengths. This investigation is being continued and the detailed results will be given later.

III.—A Theory of the Origin of Leaves.

By J. Small.

In a recent account of the elements of phyllotaxis Church, referring to "the initiation of primary ramuli" says "One may not see exactly how it is done, as a more intimate plasmic or even 'molecular' function" (6, p. 56). The present contribution is an attempt to explain the missing point "how it is done" in so far as the higher plants are concerned, and the theory might be extended with certain modifications to the marine algæ of the phytobenthon.

In the above-mentioned paper (2) it is shown that the apical meristem of the shoot may be considered to be surrounded by circular zones of potential differences. The lateral organs, such as growing leaves, can be considered as possessing similar but excentric zones of potential differences. If the E.M.F. of the stem is small compared with that of the lateral organ we may compare

the electrical conditions to those which occur when a large bar magnet is placed horizontally near the opposite pole of a small erect cylindrical magnet. Then the lines of force can be demonstrated as arranged in Figure 1, with a small neutral area on the side of the "axis" magnet opposite or nearly opposite the bar magnet which takes the place of the lateral organ. It has been suggested that the polarisation of growth in the stem is due to the normal polarity current; the cells in that neutral area would, therefore, be freed from this polarising influence, and would grow out in all directions in the fundamental spherical form, giving the more or less hemispherical primordium of a leaf. The shape and size of the leaf primordium would depend upon the relative strengths of the two electric fields.

Fig. 1. Combined electric field of a large bar magnet and a small cylindrical magnet as shown by iron filings.

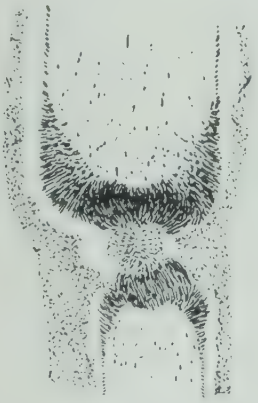

Fig. 2. Combined electric field of one large bar and one smaller bar and one small cylindrical magnet.

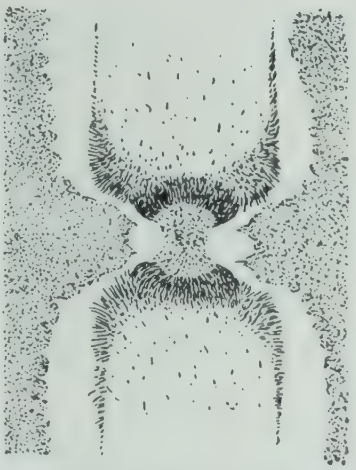

Fig. 3. Combined electric field of two equally large bar magnets and one small cylindrical magnet.

When the primordium has developed, an apical meristem is differentiated, with consequent loss of neutrality and acquirement of polarity, and a third electric field is developed (Fig. 2). The first leaf may be taken as the cotyledon, the second as a foliage leaf. The position of the third leaf or fourth electric field would then depend upon the rate at which growth caused the removal of the meristems of the first and second leaves away from that of the stem apex. Any slight inequalities of growth would result in tangential displacement, as in Fig. 2, and one primordium, not two primordia would be the result. Since these movements are part of a "continuous energy expansion system" (see 7, Chap. XX), the

arrangement on the ϕ ratio or spiral of Pheidias and the concomitant Fibonacci ratios are the natural consequences.

As a special case we have the opposite and decussate phyllotaxis (Fig. 3) where the lateral fields are equal in magnitude and in shape with the production of two equal, neutral areas arranged at right angles to the plane of the first two leaves. As these first leaves pass away by the elongation of the axis the primordia induced by them develop in their turn two electric fields which induce neutral areas and primordia directly above the first pair of leaves. These suggestions by analogy are being followed up and the results will be published later.

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MUTATIONS AND EVOLUTION.

BY R. RUGGLES GATES.

CHAPTER VII.

MUTATIONS IN ANIMALS.

IN animals, the evidence for polymorphism arising through mutation is equally extensive, and a study of any group systematically reveals innumerable instances. As with plants, many of the forms arising in this way, especially in conditions of captivity where selection is eliminated, are to be classed as abnormal, but there are many others to which this does not apply. They represent innocuous or occasionally even advantageous changes, or changes which would be advantageous in certain environments.

One of the convincing cases of an expanding polymorphic group whose various types are mutational in origin is to be found in the land-snails. Gulick (1905) studied the Achatinellidæ of Hawaii, and the consideration of isolation as an evolutionary factor is frequently based on his work. More recently Crampton (1917) has investigated the related land-snail genus *Partula* of the Society Islands. It is well known that each valley often has its own peculiar species or varieties of snails, and this is the classical case of evolution under isolation. From the later studies it has become clear that isolation is not a *factor* of evolution but a *condition* in which evolution by mutation may take place.

Crampton's extensive study of the genus *Partula* in Tahiti has led to definite and well-substantiated conclusions. Over 80,000 individuals were collected during visits in the years 1906 to 1909. Accurate records of the distribution of species and varieties had been made by Garrett in 1884, and it was thus possible to determine what changes in the snail fauna had taken place during the intervening 25 years. During this period a number of new forms have

arisen, evidently by mutations, and others have extended or in some cases retracted their area of distribution. The writer states that "mutation has been demonstrated in numerous instances, and in many species belonging to several islands." It is concluded that the morphological differences which appear are due to "spontaneous congenital causes that remain unknown in themselves" but whose effects are produced independently of environment, isolation of the forms in different valleys merely preventing an intermingling of populations.

To mention a few cases of variation in the Tahitian forms, *Partula otaheitana rubescens*, an exclusively sinistral sub-species, occurs in red and yellow varieties, the former being apparently a a simple Mendelian dominant. *P. o. affinis* has a dextral coil, but sporadic sinistral mutants occur. Similar reversals of symmetry are also known in other Gasteropods, such as *Crepidula*. In *affinis* the dimensional characters were found to vary from valley to valley. A banded form found by Garrett in a restricted locality now occurs in 20 separated regions of Tahiti, apparently as the result of independent mutations in the local populations. A red-banded form was also found by Crampton—an entirely new bicoloured pattern. Giants also appear in the sub-species *affinis* and *sinistrorsa*, and dwarfs in certain colonies of *rubescens* and other large snails. With regard to inheritance of banding in land-snails, Lang (1912, etc.) has interpreted it in Mendelian terms from breeding experiments with the European *Helix hortensis* and *H. nemoralis*.

In the plumage of birds, dichromatism or the existence of two interbreeding colour varieties, is a characteristic of many species, and the condition has apparently arisen through a mutation. As a typical case, the red and grey phases of the North American owl, *Otus asio*, have been discussed elsewhere,[1] the red being apparently a simple Mendelian dominant to the grey phase.

A remarkable case of an inherited variation in goats, which involves the nervous system, is recorded (Hooper, 1916) from Tennessee. In the central and eastern part of the State, there is a breed in which, when suddenly frightened, the hind legs become stiff and the animal jumps along. If greatly frightened the front legs also become stiff and the animal falls to the ground rigid. These stiff-legged goats are preferred because they do not jump fences, but it is obvious that in nature such a variation in any mammal with preying enemies would be eliminated by natural

[1] Gates (1917c).

selection. It seems reasonable to suggest that the so-called death-feigning instinct in many insects probably originated in the same way. So far as I know, this is the first suggestion of a mutation in an instinct. It would be selected in those insects in which such action would save their lives.

The hornless condition in cattle is another mutation of much interest. Horns are known from the palæontological record to have undergone a gradual progressive development in various groups of Mammals, while in the polled breeds the horns have apparently been suddenly lost through a mutation. Punnett[1] has suggested that the hornless condition may have co-existed in a species along with the gradual development of horns. Since the polled condition is dominant, however, at least in cattle, the recessives would all be devoid of a factor for hornlessness. And since the horns are a highly serviceable and necessary weapon of defence in the wild species, it seems very probable that the original hornless type would be stamped out by selection as soon as horns developed far enough to become a valuable weapon. This would take place whatever the causes of the progressive development of horns. There are no traces of hornless cattle before the historic era, although Herodotus describes the domestic cattle of the Scythians as hornless. In the last two centuries many hornless varieties have arisen and the origin of some polled breeds is known.[2] The hornless mutation is in a sense a reversion as regards that character, and as such is comparable with peloria in flowers. The polled Hereford breed originated from a mutant at Atkinson, Kansas in 1889.[3] Being dominant, it cannot be supposed to have been present in the germplasm before its external appearance.

An interesting and little known work by Bonavia (1895), while containing some unacceptable ideas, devotes a chapter to monstrosities as probable factors in the creation of species. Among fishes are cited the sword-fish *Histophorus gladius* with its upper jaw prolonged, *Hemiramphius* and various others with the lower jaw prolonged; also *Zygœna* the hammer-headed shark, which may have originated monstrously by a projection of both ocular regions. A hairless condition is normal in certain races of Chinese and Mexican dogs. It occurs as an anomaly in horses cattle and dogs, and hairlessness in man "may have occurred all of a sudden

[1] Mendelism. MacMillan.

[2] See MacDonald and Sinclair, 1882. History of polled Angus cattle.

[3] Walter, H. E. Genetics, MacMillan, 1913.

as a monstrosity." Featherless birds are not unknown, or only certain pterylæ may be affected, as in the bareneck fowls (Davenport, 1914), a condition which is dominant in crosses. A well known case cited by Stebbing is that of *Dorippe dorsipes* with four legs, and four more small ones on its back. It is therefore clear that even mutational monstrosities have played their part in the production of species, and it is quite certain that if some family and ordinal characters could have been seen at their first appearance they would have been considered monstrosities.

Dwarfs and giants are as common in animal species as among plants. A dwarf-bearing strain of guinea pigs is described by Miss Sollas (1914). It produced in all 192 normals to 64 dwarfs, the latter evidently behaving as a simple Mendelian recessive. The study of inheritance of melanism in British Lepidoptera has in recent years attained considerable proportions. These results can only be touched upon here, but they show that the melanic variety usually behaves as a Mendelian dominant, sometimes a recessive, and in certain cases gives blending inheritance. A number of cases are discussed by Bateson (1913, p. 135 ff.)

Sumner (1917) has obtained mutations in the Californian deer-mouse, *Peromyscus maniculatus*, both in the wild state and in captivity. A "yellow" mutation of *P.m. gambeli* was trapped at LaJolla, California in 1914. The normals have a dark gray pelage and black eyes. In cages a total of 14 normal to 7 yellow appeared, in broods which were traced back to a single pair of grandparents. There were no other yellows among over 400 *gambeli* bred. Hence the appearance of the yellow was due to a recessive mutation factor carried in the two grandparents. Castle has reported similar "yellow sports" in wild species of *Microtus*.

CHAPTER VIII.

Limitations of the Cell Theory.[1]

The work of the present century in experimental breeding and cytology has led to many new points of view and new lines of approach to old problems. It therefore seems desirable to examine our present bearings from the point of view expressed in previous chapters. That the experimental method of attack upon the problems of variation and heredity, as well as those of embryology, is sound and of the utmost value cannot be gainsaid. On the other hand, it does not follow that the older conceptions of evolution, natural selection, and the inheritance of acquired characters are necessarily unsound or, if adhered to, subversive of the modern experimental results. We wish to show (1), that the experimentalist point of view resulting from the work in mutation and Mendelism is frankly antagonistic to the views of many palæontologists, anatomists and others who deal with the non-experimental data of evolution involving orthogenesis and the inheritance of acquired characters (2), that while these two factors bear entirely different relations to evolutionary changes, both are necessary to account for evolution as it has taken place.

It may be said that the divergence between the geneticist point of view and that of the biologist who relies upon the historical background of evolution for his interpretation of evolutionary factors has long been manifest; and that is true. Yet we venture to think that no one has clearly visualized or set forth the fundamental character of this antagonism in relation to the structure of the organism. Moreover, those who have recognised the opposition between the principles of germinal variation and inheritance of acquired characters in evolution have usually endeavoured to solve the difficulty by denying or ignoring one principal and affirming the other. Rather, we think it necessary to harmonize these two conflicting views into a more complete and balanced conception of the evolutionary process.

We propose, then, to show that higher organisms exhibit two sharply contrasted types of characters which differ fundamentally, (1) in their manner of origin, (2) in their relation to the structure of the the organism, (3) in their relations to such phenomena

[1] The following chapters are chiefly based on a discussion "On the Existence of two fundamentally different types of characters in Organisms," which took place at the Linnean Society, February 5th, 1920.

as recapitulation, adaptation, inheritance, and distribution. The first class of characters are (as already expressed in Chapter II.) cell-characters, which have arisen through mutations, are represented in every cell of the organism, and are usually inherited as distinct units. Since they arise in and are carried by the nuclei they may be called *karyogenetic*. To the second category belong characters which arise gradually in the organism through impact of the environment or through "orthogenesis,"[1] may apply only to localized portions in the life-cycle of the organism, and at first are not incorporated in the germplasm. Such characters we may call organismal[2], in contradistinction to cell-characters. Organismal characters may imply an increase in the length of the life-cycle, as strikingly evidenced in so many animal larvæ which undergo metamorphosis, or they may show stages in shortening, as in the gametophytes of many higher plants.

The attitude of experimental biologists to the questions of recapitulation and inheritance of acquired characters (although the former has never fallen into the same disrepute as the latter) has been generally one of skepticism and denial. Reasons for adopting a different position may be given as follows: (1) the difficulty of explaining adequately the abundant facts of recapitulation in plants and animals by means of mutations or changes originally germinal; (2) the logical necessity of the principle of functional inheritance in some form to explain the origin of embryonic recapitulatory characters involving adaptation; (3) the approach to an understanding, through such agencies as hormones and enzymes, of how the transmission and ultimate germinal fixation of somatic modifications may take place; (4) the slowly accumulating direct experimental evidence for parallel induction and the transmission of modifications.

In contrasting organismal with cell characters we are contrasting two points of view regarding the organism which are at least as old as Aristotle and Empedocles. Modern representatives of these views speak of the organism as a whole on the one hand, and of elementalist or particulate theories on the other. It scarcely needs pointing out that elementalist conceptions, particularly of

[1] An orthogenetic result may also of course arise from a succession of germinal changes or mutations following each other in any line of phylogeny.

[2] In the Linnean discussion, Professor F. E. Weiss suggested the obvious antonym *cytogenetic* for this category of characters, since they are apparently cytoplasmic in origin. This term had already been considered, but was finally discarded because "organismal" expressed better the idea desired. Nevertheless it will be a useful term in certain connections.

heredity and variation, have had a wide vogue in recent years. On the other hand, Loeb (1916) and from a different point of view, Ritter (1919), among others, have recently championed the organism-as-a-whole. The latter writer has pressed this view farthest, in the endeavour to eliminate elementalist conceptions altogether. We believe a truer attitude lies in the recognition of a fundamental truth in both these aspects.

In a former work[1] and in earlier chapters of this series we developed a cell theory of mutations emphasizing the fact that each new form arises as a germinal *difference* from the parent type. The cell unit, in all such variations, is the thing which has changed, and the new external characters which appear in every part of the organism are the structural result of an ontogeny built up with a different unit as basis.[2] This situation was particularly clear in *Œnothera gigas*, where it was shown[3] that the volume of the nuclei and cells has increased in varying proportions in different tissues. Tupper and Bartlett (1916) have confirmed and extended these results in the case of *Œ. stenomeres* mut. *gigas* which is also tetraploid or $4x$ in the constitution of its nuclei.

Without going farther afield for confirmatory data, which are amply furnished in the contemporary literature, we may conclude that the mutation theory of germinal variations is firmly grounded upon the cell theory, and if the cell theory were universal in its application then mutations or germinal changes might be supposed to supply the whole of the material for evolution in organisms. Facts such as those pointed out above lead to the concept of the species cell. This is a conception which has been independently arrived at by different lines of approach (see, for example, Lang, 1909). It is a sounder and less extreme conception than that of the organism as a cell-state, *i.e.*, merely an aggregation of more or less independent cell units.

Biologists have long recognized the necessity for limitations of the cell theory of organic structure. On the one hand we have the legitimate and necessary conception of the species cell, briefly set

[1] The Mutation Factor in Evolution.

[2] If this be the case, then the mitoses during ontogeny do not bring about the unequal division and sorting out of portions of the chromosomes, as Weismann supposed; but all these divisions are, as they appear, equational so far as the chromosomes are concerned. This conclusion has also been reached from the study of experimental embryology (Conklin, 1916) and from other lines of approach. So far as the chromosomes are concerned, their materials are apparently not as a rule segregated by differential divisions during ontogeny. On the other hand, differential divisions of the cytoplasm are of frequent occurrence.

[3] Gates, 1909a.

forth above, implying that germinal changes arise in a fixed life-cycle through a change in the cell unit which is represented in every nucleus and therefore may modify every stage of the new organism.[1] On the other hand, if the more fundamental facts of recapitulation mean anything, they imply that at some time an actual lengthening of the life-cycle has taken place, either by the addition of cell divisions at its end or by their intercalation at some point. Such a process can not easily be accomplished by a variation in the structure of the cell or nuclear unit itself, but must rather be the result of the organism as it were overcoming its cell shackles and by its own energy producing new developments, though such novel additions are themselves cellular in structure.

From the time the foundations of the cell theory were laid by Schleiden and Schwann in 1838-39, its universal sway was scarcely questioned for over half a century. During this period it was established that cells arise only from the division of previous cells, and the cell theory culminated in such conceptions as the physiological division of labour among cells, the mosaic theory of embryonic development, the individual as the sum of the activities of its various cells. In short, it came to be assumed that cells make the organism, while the contrary fact that the organism after all makes its cells was tacitly or explicitly denied. In the same way it was assumed that each cell of a multicellular organism necessarily corresponded with the whole organism in the Protozoa.

One of the first reactions from this extreme development of the cell theory, which made the organism not a master in its own house but a slave of its constituent cells, was a well known paper by Sedgwick (1894) on the inadequacy of the cell theory of development. His views were based on studies of the embryos of *Peripatus capensis*, which he believed were essentially cœnocytic in structure; also upon the development of mesenchyme and nervous tissue in Elasmobranch embryos. As far as Peripatus is concerned, delicate cell walls have recently been demonstrated (Glen, 1918) both in the ectoderm and endoderm layers, by careful preparations and the use of an immersion lens. But their demonstration does not affect the fundamental question of the relation of the cell to the organism, for, to mention only a few cases, it is well known that in the formation of the blastoderm of the insect egg, as well as in the early stages of development of the female gametophyte and proembryo in Gymnosperms, a stage is passed through in which

[1] It appears that, especially in animals, the change is frequently visible or obvious only in certain organs.

there is multiplication of free nuclei,[1] which arrange themselves in a particular manner, but without the formation of cell walls until later. That cells can develope within a cell is also well exemplified in the development of the embryo-sac of Angiosperms.

In the same year Whitman (1894), in a notable paper, attacked the cell theory on fundamental theoretical grounds. He concluded that the formation of the embryo is not controlled by the form of the cleavage. "The plastic forces heed no cell-boundaries, but mould the germ-mass regardless of the way it is cut up into cells." His position was that "organization precedes cell-formation and regulates it."

It is impossible here to enter into a discussion of the various views which grew out of the extensive studies on cell-lineage, but granting the accuracy of the above limitations of the cell theory, it will be seen that they are in no way out of harmony with the view of mutations as cell variations, or rather nuclear variations, previously expressed. Another limitation of the cell theory will be considered in the next chapter.

[1] Incidentally it may be pointed out that any comprehensive theory of heredity must be one which is applicable equally to those cases in which regular cleavage of the egg takes place and those in which in one stage the embryo contains free nuclei. Since the nuclei are the only structures in common, and the laws of inheritance remain the same in both cases, *ergo* the nuclei and not the planes of cleavage must determine those laws.

CHAPTER IX.

The Recapitulation Theory.

The recapitulation theory has had many vicissitudes both in its application to plants and to animals. The conception has been stated and restated many times in varying terms, but that ontogenetic stages may have a phylogenetic significance has rarely been denied and has more often been implicitly assumed. The principle was tacitly recognized even before Darwin, and he accepted it practically without reserve. Indeed it was one of the foundation stones in his argument for evolution.

It is desirable also to point out that any theory of recapitulation which is to have any significance in the interpretation of life histories must recognize that in the last analysis recapitulation implies that at some stage in the evolution of any group an increase in the life-cycle took place, by the addition of certain stages. This is in sharp contrast with a germinal change, which necessarily modifies every stage, at least internally as regards nuclear structure, but can hardly be held to add anything to the adult stage of development, or in other words to increase the number of stages in the life-cycle.

Recapitulation and the alternation of generations in plants.

As regards plants, it may first be pointed out that the theory of the antithetic alternation of generations, which has been widely adhered to by botanists and has been given its most notable expression in the classic volume of Bower (1908) on *The Origin of a Land Flora*, implies from the evolutionary point of view a continued lengthening and increase in complexity on the part of the sporophyte, and in seed plants a contemporaneous shortening and simplification of the gametophyte. This theory runs like a golden thread through all the speculations concerning the origin and larger relationships of the main groups of vascular plants, and there is nothing quite corresponding to it among animals. In the able hands of Bower, it implies that the sporophyte generation resulting from the fertilized egg is intercalated between two gametophyte generations and has gradually increased in complexity or length through the Bryophytes, Pteridophytes, Gymnosperms and Angiosperms in connection with their gradual transition and adaptation from aquatic or moist to typically terrestrial conditions.

True, the theory of homologous alternation in plants has also been held, though not so widely. It was for a time based chiefly

on the facts of apogamy and apospory in Ferns, and experimentally induced apospory in Bryophytes (Lang, 1901). But even when of natural occurrence, these are generally admitted to be exceptional conditions of recent development. The careful cytological studies of apogamy and apospory, however, led Farmer and Digby (1907) to the conclusion that these phenomena leave the question of alternation essentially where it was. It need only be pointed out here that the theory of homologous alternation of generations in plants corresponds to such a view as would restrict the significance of recapitulation to a great degree; while an important phase of the antithetic theory is that it implies a *lengthening* of the sporophyte generation in connection with the adaptation of plants to a terrestrial habitat.

In his original studies of apogamy and apospory, Lang (1898) carefully refrained from giving his views a bias in either direction. More recently (Lang, 1909) he has propounded an interesting conception of homologous alternation from an ontogenetic point of view.[1] Briefly the view begins with the concept of the species cell, based on the fact that any cell of the species is potentially able to reproduce the whole plant. This being the case, "the haploid and diploid germ-cells have potentially the same morphological properties." But they are believed to develop different generations because the germ cell is exposed to different conditions in initiating the two generations. This interesting suggestion, however, encounters many serious difficulties, some of which were pointed out in a criticism by V. H. Blackman (1909).

It cannot be said that the homologous view has received wide support as regards Archegoniates and their descendants, but on the other hand important evidence has developed for the occurrence of homologous alternation in Algæ. It is significant that in this group the gametophyte and sporophyte generations develop under the same relatively uniform conditions, exposed to sea water, and they are morphologically alike. Without discussing the subject in any detail,[2] it may be pointed out that Yamanouchi (1906) found in the red alga Polysiphonia an alternation of generations, which he regarded as antithetic, between tetrasporic plants having 40 chromosomes and sexual plants with 20, the cystocarp being a part of the sporophytic phase. Lewis (1909), in a study of another of the Rhodophyceæ, Griffithsia, has taken up a more advanced position

[1] See also the discussion on alternation of generations at the Linnean Society, published in NEW PHYTOL. 8: 104-116, 1909.

[2] For recent discussions of the life-cycles in Algæ see Fritsch (1916) and Davis (1916).

which appears to be well justified by the facts. The life history of Griffithsia is in general parallel to that of Polysiphonia, the tetrasporic plants apparently having 14 chromosomes and sexual plants 7, though there is some doubt about the accuracy of these counts.

According to the views of Lewis, there is (1) an antithetic alternation between sexual plants, representing the gametophytes, and the sporogenous cells of the cystocarp, representing the sporophyte, (2) a regular succession of tetrasporic and sexual individuals representing an homologous alternation of generations but not equivalent to the alternation in Archegoniates. He believes that the tetrasporic plant has been intercalated in the life history, not through the "gradual differentiation of a simple product of the germination of the zygote," which is the pith of the antithetic theory; but, as Yamanouchi suggested, through the suppression of chromosome reduction in the formation of a carpospore which then at once grew into a tetrasporic plant.

In concluding a brief survey of this very large subject of alternation, we may remark that the antithetic theory, which continues to receive the larger number of adherents, implies just such a lengthening of the life-cycle as is indicated by recapitulatory phenomena. The homologous theory, on the other hand, would account for the alternation through the sudden intercalation of a generation in Algæ as the result of a change in spore development which is essentially mutational. In Archegoniates, the homologous view would apparently imply the gradual simultaneous progressive differentiation of gametophyte and sporophyte through differences in the environment in which the asexual spore and the fertilized egg develop. But as Farmer[1] has pointed out, it is impossible to imagine how the Bryophyte sporogonium at any rate could have arisen through modification of the gametophyte. It seems clear that this structure at least must represent an intercalated phase progressively developed. Each group of plants must then, as Farmer has emphasized, be separately considered on its own merits, on the basis of the historical probabilities as determined by comparative morphology.

Recapitulation phenomena in Gametophytes.

It may be noted in passing that although plants "climbed out of the water" at a remote period, yet large groups of Bryophytes and Pteridophytes still survive although imperfectly adapted to life on dry land. This, as Bower points out, is probably because the

[1] New Phytol. 8: 113, 1909.

sporophyte has developed far enough to make possible the production of spores in sufficiently large numbers to ensure the passage through the difficult stage in the life-cycle when water is a necessity for the accomplishment of fertilization. Only in vascular plants above the Cycads has complete adaptation to terrestrial conditions been accomplished, by the adoption of siphonogamy and the loss of swimming sperms.[1] Nevertheless, the higher siphonogamous plants do not, except in rare instances, show recapitulation stages of their gametophytes. In other words, the gametophyte development is usually direct. This can hardly be because the gametophyte in its later evolution forms a reduction series, because among animals the most remarkable and convincing instances of recapitulation occur where degeneration has taken place as a result of parasitism or the adoption of sedentary habits. Typical recapitulation phenomena do nevertheless appear in plant gametophytes. For instance the archegonium, which is so characteristic an organ in Bryophytes, and has given an aggregate name to the three great groups in which it occurs, persists in a progressively reduced form throughout the Gymnosperms until we reach the higher Gnetales, although in certain Araucarians (Eames, 1913) it has become a positive hindrance to fertilization. In this case the archegonium neck cells have developed into a thick-walled structure which the pollen tube cannot penetrate. But the jacket-cells adjacent to the neck are actually eliminated, thus making it easier for the pollen tube to reach the central cell. No more striking case could be cited of the continued production of an organ which not only has lost its function but which is a positive hindrance to the functioning pollen tube, though its retention has entailed other structural changes in the jacket-cells to facilitate fertilization.

Thus throughout the Gymnosperms, the gametophyte is being reduced, and recapitulation phenomena which suggest an ebbing tide occur in its terminal stages. The archegonium itself shows a gradual series of reduction stages until it is finally eliminated. In the lower Gymnosperms it has already lost the neck canal cells found in the archegonium of Mosses and Ferns, and among the Conifers the ventral canal cell is gradually eliminated. In the Abietineæ (see Coulter and Chamberlain, 1910) a ventral canal cell is cut off, in the Araucarians the nuclear division takes place but no cell wall is formed; or in some species of Pinus a wall may be

[1] It is well known that similar types of adaptation from aquatic to terrestrial conditions have occurred in the Fungi, involving the loss of free swimming gametes and the development of some form of siphonogamy.

formed in some instances and only a nucleus in others. In every case this ventral canal cell or nucleus is only a reminiscence which continues to reappear as a terminal stage although in its origin it dates back at least to the Liverworts. But it appears to be finally eliminated in the Taxodineæ. The cases just cited, however, do not involve recapitulation so far as the individual ontogeny is concerned. They are only seen to be closely related to such phenomena from a comparative phylogenetic point of view.

Such a reduction series Coulter (1915) no doubt justly considers to represent the expression of an orthogenetic tendency, though whether it is the result of climatic differentiation is not so clear. The series derives its interest from the fact that the higher Gymnosperms, in which the archegonium is quite eliminated, must have had ancestors in which that reduction gradually took place. From our present point of view, the explanation cannot be found in a series of successive nuclear variations or mutations, for these would make themselves felt in other parts of the organism, affecting many characters in a correlated fashion. Though the argument is by no means conclusive as regards this matter, yet it seems most reasonable to consider these as organismal characters and to explain the shortening of the gametophyte generation in the same way that recapitulatory characters find their explanation. The direction in which that explanation is to be sought will be discussed below.

Another support for this view may be found in the fact that the chromosome number is remarkably uniform throughout the Gymnosperms, being, with few exceptions, 24. If the evolution of the Gymnosperms had taken place largely through mutations, *i.e.*, through changes arising in the germinal chromatin, one would expect it to have produced some effect on the chromatin morphology in the various species. The Angiosperms, by contrast, in which there is evidence that much mutation has taken place and is now going on, are characterized by remarkable variety in number, size and shape of their chromosomes even within single families or genera. The same is true of insects.

Other cases of ancestral reminiscence in gametophytes, as though the organism repeated certain stages from force of habit or from some source of energy impelling its development forward, are to be found in Angiosperms. In the nuclear divisions within the embryo sac an evanescent cell-plate sometimes appears on the spindle. But this reminiscence of wall-formation soon disappears along with the spindles. The same is true of the prothallial cells

in the male gametophyte of many Gymnosperms. There is one such cell in Cycads, which persists. Ginkgo has one ephemeral and one persistent prothallial cell which are cut off in succession by the side of the microspore, while in Pinus both prothallial cells dwindle promptly to small dark-staining masses, as though the life had quickly gone out of them. The nucleus may begin to disorganize even before the cell-plate is formed. Such structures represent momentary stages of an ebbing tide. In *Picea canadensis*, Hutchinson (1915) has found all these and other conditions to occur as variations.

Recapitulation in the Sporophyte.

If now we turn to the sporophyte, we find again many of the most striking cases of recapitulation in Gymnosperms. Indeed they appear to be of more frequent occurrence in this group than in any other plants. A possible reason for this has already been suggested, namely the relative infrequency of mutations. It is well to keep in mind also that recapitulation in the sporophyte usually indicates adaptation to altered conditions. Among well known instances in Conifers may be cited the genus Phyllocladus, characterized by an absence of leaves, the branches forming flattened leaf-like expansions. The seedlings, however, have a terete axis bearing ordinary leaves and this obviously represents the ancestral condition, from which for some unknown reason the genus departed. That such an alteration is not mutational is indicated, according to the present interpretation, by the fact that the ancestral condition is thus clearly present in the earlier stages of ontogeny. A mutational change, being represented in every nucleus from the fertilized egg onwards would have eliminated, or rather transformed, this juvenile stage. In Œnothera, as de Vries (1909) pointed out, the first leaves after the cotyledons make it possible to recognize a mutant form.

To mention three other cases of recapitulation in Gymnosperms: A feature of the genus Pinus is the occurrence of dwarf shoots, each bearing a fascicle of needle leaves. But in the seedling the leaves are scattered on the stem as in other conifers. Similarly the genus Larix, unlike most conifers, has deciduous leaves; but in the juvenile stage the leaves adhere for several years. In the Mariposa grove near the Yosemite valley in California I observed that *Sequoia gigantea* is a number of years old and many feet high before its foliage acquires the characteristic appressed form. When grown in the English climate, this appressed type of foliage appears never to be quite reached even in old trees.

Other writers have carried the principle of recapitulation much farther, and notably Jeffrey (1917), who applies it to the histological structures of vascular tissues, and further finds that regeneration after wounding frequently leads to the reappearance of ancestral characters. This principle is freely used by him in the comparison of living with fossil forms, and in the interpretation of phylogenies. To cite examples from the Araucarian conifers, it has long been known (Thistleton-Dyer 1901) that in the adult stem of these trees, owing to the continued activity of a cambium the leaf traces have the peculiarity of being persistent for many years after the leaves have fallen. Another well known peculiarity of Araucarian wood is that the bordered pits in the xylem tracheids are alternate in origin, not opposite as in other living conifers. Jeffrey (l.c., p. 236) points out that in Mesozoic araucarian woods belonging to the genus Brachyoxylon the leaf traces persist only for a short time, and the bordered pits are not alternating and crowded as in the living genera. In seedlings of the modern Agathis and Araucaria, however, " the leaf trace persists only so long as it is related to a functional leaf," and the pitting is like that found in the Cretaceous Brachyoxylon. Such a striking case of recapitulation—and others of like nature are known—can hardly find its explanation in a germinal change which belongs equally to every cell.

While these principles of recapitulation seem for the most part well established, caution must of course be used in their application, especially in these more complicated cases; for it would be easy to deduce incorrect phylogenetic conclusions by attaching more significance to such cases than they really possess. It is important also not to lose sight of the fact that recapitulation phenomena occur where there has been adaptation to new conditions. Such changes are often climatic, but may also be environmental in the widest sense.

One instance of more doubtful recapitulatory phenomena in plants must suffice. In a recent paper on Rhododendron seedlings, Professor Balfour (1917) has shown that many of the species in their earlier years pass through a series of changes in the pigmentation and pubescence of their leaves. Thus in *R. adenogynum* Diels the under surface of the leaves is red glandular in the seedling. But about the third year the redness disappears as well as the glandular hairs. After some seven years the buff-coloured tomentum of long, interwoven, branched hairs begins to show at the base of the (now green) leaves, and gradually in later years

covers the whole under surface of the leaf. Similar developmental changes take place in a number of other species.

Balfour thinks this developmental modification is in relation not to a climatic change in the habitat of the species, but to the differences in environmental conditions as regards, light, moisture, heat and air currents encountered by the leaves of the young plant near the soil and of the older plant at a higher level. He points out that a higher temperature and a more rapid metabolism (subserved by anthocyanin) are important at first, while control of transpiration (subserved by tomentum) is important later.

The above case could not be regarded in itself as evidence of recapitulation, but it serves to show how indubitable recapitulatory phenomena shade into those which have only a physiological or ecological rather than an ancestral significance.

Summarizing the data of recapitulation in plants, we may say that recapitulatory characters are found chiefly (1) in the seedlings of Gymnosperms and some Angiosperms, (2) in the terminal stages of gametophytes, (3) in wood structure; but as a rule they have been lost from the ontogeny through the cellular development becoming direct. If the antithetic theory of alternation of generations be correct, however, then a large part of evolution has been concerned with the gradual development of characters which were originally organismal and have become in some measure recapitulatory.

Recapitulation in Animals.

Important and significant as are the indubitable cases of recapitulation in plants, the phenomenon is much more prevalent in animal development. This may perhaps be connected with the fact that the animal in development may be said to have greater power over its cells owing to their thinner walls and greater plasticity.[1] A striking phenomenon in the cleavage of animal eggs is the mutual readjustment of the cells with relation to each other which goes on after each cleavage.[2] In this way the forces of the

[1] A number of facts indicate that in some respects animals have greater powers of regulation than plants. One need only mention (*a*) phenomena of metamorphosis in which tissues may break down and be used again in the building up of new structures; and (*b*) the fact that in Metapodius (Wilson 1910) and Drosophila (Bridges 1916) the presence of one or even several extra chromosomes (duplicates of one member) in the nuclei produces no external alteration; while the duplication of one chromosome in Œnothera produces striking external differences. The recent studies of Rosenberg (1918) on Crepis indicate that here also the duplication of a pair of chromosomes alters the external features of the plant.

[2] It is a well known fact that cleavage itself is a rhythmic process, in which a period of simultaneous nuclear division alternates with a period of nuclear growth, and this rhythmic alternation is accompanied by a physiological rhythm in CO_2 production, permeability, etc.

organism can, as it were assert a power over the cells in maintaining a unity of structure during development to a degree which is not possible with the thicker cellulose walls of plants, though in woody stems growth-pressure produces a certain amount of such readjustment of dead cells. In any case, whatever the reason, it remains true that while development in plants is usually direct, and recapitulation the exception, the animal embryologist is confronted with recapitulation on all hands with such amazing profusion that a comprehensive principle is more obviously required for their explanation.

Another explanation of the difference between plants and animals in the occurrence of recapitulation may lie in a greater frequency of mutations in the phylogeny of plants. Also, animal groups in their evolution have probably passed more frequently by adaptation from one habitat to another. Witness, for example, the number of groups from Ephemeridæ to whales or penguins which have become secondarily modified for an aquatic life. Even when a like occurrence happens in plants, the stages of it are often nearly or quite obliterated by short-circuiting. It is therefore quite unsafe to argue in the case of plants that because a given adaptational character shows no recapitulation in development it must have originated through a germinal change. Such an attitude stands a better chance of being sound in the case of animals.

Concerning the facts of recapitulation, MacBride's textbook of embryology—Invertebrata (1914) is a veritable mine of information. His attitude represents a return to an interpretation of the significance of larval stages in relation to phylogeny on a frankly neo-Lamarckian basis. Embryologists of the last two decades have largely endeavoured to avoid this attitude, but without conspicuous success. MacBride assumes that larval stages represent actual ancestral groups of organisms. It is also significant, as we pointed out in the case of plants, that the recapitulation seems always to have originated in connection with the adaptation of the animal to a new set of conditions.

Although we have never seen it explicitly stated that embryonic recapitulation implies the inheritance of acquired characters,[1] yet it is probably the tacit recognition of this fact which has led to the denial of recapitulation by those who believe only in germinal variations as material for evolution.

[1] Since this was written I have received from Professor MacBride (1917) a paper which I had not previously seen, in which it is definitely stated that recapitulation implies the inheritance of acquired characters, and citing a number of cases in support of this view.

Zoologists are generally agreed that the nauplius and zoæa larvæ of Crustaceans and the veliger larva of Molluscs represent ancestral stages; similarly, that the trochophore larva of Annelids and Molluscs shows these two very divergent groups to have been derived from a common ancestor. MacBride would go further and say that the trochophore is a smaller and somewhat reduced or specialized representative of that ancestor. According to the interpretation here adopted, the various larvæ at one time represented *terminal stages* in their respective life-cycles, and by subsequent evolution they were not modified out of existence or out of recognition through germinal changes, but became subterminal through the *addition* of later stages to complete the ontogeny. In a field where every larva has its ancestral significance, it is almost invideous to single out particular cases for illustration. The tadpole of Ascidians, which gave the first hint of the Chordate affinities of this group, is a striking instance. Only the degeneration and special adaptations resulting from the adoption of a sedentary life can account for their remarkable transformation, and we fail to see how it can be adequately explained except on a neo-Lamarckian basis. An equally irrefutable case of recapitulation is that of the feather-star Antedon, whose egg developes into a free-swimming larva which later becomes fixed by a stalk. This fixed stage corresponds with the modern genus Pentacrinus. The adult feather-star developes cirri and, losing its stalk, becomes free again. Can anyone pretend to believe that this remarkable series of transformations does not recapitulate the history of the race? And, if so, how can one avoid the conclusion that the life-cycle has been lengthened?

A type of recapitulatory character corresponding to the appearance of evanescent stages in the gametophytes of the Gymnosperms, is found in certain nauplius larvæ. MacBride (l.c. p. 204) regards the nauplius as representing the common ancestor of all Crustacea. He says, "When the larva does not hatch out as a nauplius, a cuticle is produced and shed by the embryo whilst still within the egg shell when it reaches the nauplius stage, thereby showing that formerly this stage must have been passed through in the open, in the ancestors of the forms in which it is now purely embryonic." Again, in the oyster, which has no foot and becomes permanently attached by one valve of its shell, the veliger larva nevertheless possesses a functional foot which is therefore a recapitulatory character.

Perhaps the most convincing of all cases for a Lamarckian interpretation of recapitulation is that of the parasitic Copepod, *Achtheres ambloplitis*, where as MacBride remarks, "we may almost say that the ancestor is known." The adult is a parasite on the gills of the rock-bass, and is a sac-like organism devoid of all semblance of Copepod structure, yet the animal passes through a brief larval stage which anyone would recognize at once as representing a typical Copepodan genus. Whatever explanation applies to this remarkably clear case must also apply *mutatis mutandis* to the whole series of larval stages which represent the remoter ancestry in other organisms. We think this case furnishes one of the clearest evidences of the sharp contrast we are endeavouring to draw between recapitulatory and mutational, or in other words, between organismal and karyogenetic characters. Yet it is admitted that even in this Copepodid larva there are modifications from the typical details of Copepod structure. But they follow the usual lines of diminution in size of the larva and consequent reduction in the number of metameric parts. Another factor which tends to obscure ancestral stages is the well-known principle of telescoping, or the earlier appearance of embryonic organs, which has been called heterochrony by Lankester, or tachygenesis by French writers (Perrier and Gravier, 1902). That embryonic and larval stages can also undergo special modifications of an adaptational nature is another well recognized principle which tends to obscure ancestral relationships.

Many of the battles of recapitulation have been fought over the frog, so we may briefly examine his case. Some embryologists have gone so far as to deny any ancestral significance to the tadpole. While the other extreme view, that all larval characters of the frog have ancestral significance, is certainly disproved; yet the truth evidently lies in a recognition of the fact that in the tadpole as in most other larvæ, there are some recapitulatory or palingenetic characters and some adaptational or cœnogenetic characters. The obvious recapitulatory characters are the fish-like tail, gill arches and blood system. It seems impossible to avoid the conclusion that these were once terminal developmental stages, in the frog's fish-ancestor. On the other hand Boulenger (1918) has pointed out that tadpoles have had an evolutionary history of their own and have developed special adaptational features. He enumerates (Boulenger 1897) "The horny beak and circular lip with its horny armature, the spiraculum, the enclosure of the fore-

limbs in diverticula of the branchial chambers, and such special adaptations as the ventral disc or sucker of certain mountain forms." The existence of such adaptational characters is supported by the fact that certain species differ more widely in their tadpoles than in their adult stages. Thus (Boulenger and Annandale, 1918) the Indian species *Rana tigrina* and *R. cancrivora* are so similar as frogs that the latter was classed as a variety of the former. But Annandale (l.c.) has shown that the tadpoles differ markedly in buccal armature. Whether this is a case of convergence of the adult species, as Dr. Annandale thinks, or divergence of the tadpoles, as Dr. Boulenger believes, need not concern us here, though from analogy the latter interpretation appears more probable.

To return to the recapitulatory characters, the transformation of the fish-like gill-arches of the tadpole into the aortic arches of higher vertebrates is too well known to require comment here, except to point out that it comes about through the gradual substitution of one series of blood vessels for another, the branches to the gills being gradually pinched off and the blood stream diverted to the more direct route to the lungs. The specious argument that the development of any recapitulatory character *must* go through such preliminary stages for purely structural developmental reasons is now seldom heard and can very well be consigned to oblivion. Developmental mechanics as well as comparative embryology tell strongly against it.

The experiments of Gudernatsch (1914) in greatly retarding or hastening the time of metamorphosis by feeding tadpoles on thymus or thyroid respectively, showing that growth and differentiation are separate factors, do not affect our present interpretation. They merely indicate that the processes of development and metamorphosis are physiologically controlled by something in the body of the nature of hormones or enzymes secreted by certain tissues. A recent paper (Morse, 1918) has attempted a further analysis of the processes that lead to atrophy of the tail in metamorphosis. The writer concludes that autolysis is the primary physiological factor. The first step in atrophy, according to Barfurth, is the growth of the pygostyle which, by occlusion of the blood vessels in the tail, causes an accumulation of CO_2 and acids. This acidosis of the tissues induces autolysis. In this condition the phagocytes are chemotactically attracted to the atrophying organs, so that phagocytosis is a secondary, and not the primary factor as Metschnikoff supposed. Hormones or enzymes probably stimulate

the development of the pygostyle, but something must in turn determine the development of these. Morse concluded from his experiments that it is possible to suppress metamorphosis, but that it cannot be induced in stages *far* removed from those in which it would normally occur. A certain cycle of events determined by heredity is necessary before any stimulating agent will cause metamorphosis.

Although we have spoken of recapitulatory characters having been at one time terminal stages in the life-cycle, yet it appears that they have not always been added terminally but have often been intercalated at a subterminal or earlier stage. Thus in plants the sporophyte ends inevitably with sporogenesis, so that the lengthening of the sporophyte generation must always have taken place through the addition of subterminal stages, involving the delay of sporogenesis.[1] In animals, too, spermatogenesis or oogenesis is usually delayed until the ontogeny is complete, although the greater freedom of the germ cells in their relation to the soma makes possible the occasional occurence of pædogenesis or reproduction by larvæ.

In concluding this chapter it may be pointed out that the phenomena of recapitulation furnish another limitation of the cell theory, recapitulatory characters being organismal, and embryonic recapitulation apparently involving the inheritance of functional modifications.

[1] This is a little different from Bower's well-known view of the sterilization of potentially sporogenous tissue.

CHAPTER X.

Inheritance of acquired Characters.

In the last chapter it was pointed out that adaptational recapitulatory characters have apparently not originated directly through chromatin variations, but indirectly *via* the cytoplasm. Under the influence of Weismann's conception of continuity of the germplasm, the very possibility of acquired characters or impressed modifications being inherited, was denied. Like so many other useful biological conceptions this was pushed to an extreme, and a non-existent degree of isolation and insulation of the germ cells from the soma was freely assumed. But in the last decade there has been an increasing tendency to adopt a more reasonable attitude to these problems. Weismann's conception of blastogenic and somatogenic variations or characters has also tended to lay too great emphasis on a distinction which can scarcely be said to exist at all in plants, except in sporogenesis, namely the segregation between germ cells and somatic cells. The contrast we have ventured to draw between karyogenic or nuclear characters and organismal or recapitulatory characters, seems more in accord with our present knowledge of the development, cytological structure and genetic behaviour of organisms.

In the meantime, experimental evidence for the inheritance of acquired characters and related phenomena has been slowly accumulating, but space will permit of reference to only a few papers. We may first mention Agar's (1913) work on parallel induction in the Daphnid, *Simocephalus vetulus*, where references to the related literature will be found. Agar discovered that when Simocephalus is fed on a culture of Protophyta the valves of the carapace became reflexed, the degree of this abnormality gradually increasing during successive instars or moults. If such individuals were removed to normal conditions before their (parthenogenetic) eggs were laid, these eggs nevertheless developed into adults showing the same abnormality which their parents had acquired ontogenetically through environmental impress. But the effect soon wore off in later generations grown in normal conditions.

Similarly, grown at higher temperature the animals were very much smaller, developed more rapidly and produced smaller broods. Eggs laid shortly after removal to ordinary temperature developed into adults nearly as small as their parents, but in F_2 little of the effect remained.

The parallel induction in germ and soma is believed to be brought about by "altering the nature of the metabolic products included in the living protoplasm." That such effects are transmitted for one or two generations is an excellent example of a cytoplasmic effect temporarily inherited, and indicates that minimal quantities of such substances are multiplied so as to produce a powerful effect. Kammerer claims to have obtained such a result in experiments with a lizard, where the character white instead of red belly, impressed by high temperature, was transmitted through the *sperm* to the next generation of adults.

The experiments of Kammerer (1909, 1919) with *Alytes obstetricans* have been much discussed. His recent results are largely confirmatory of earlier papers published ten years ago, and a number of other contributions, including an elaborate series of experiments with salamanders, have appeared in the intervening years. It is well-known that Alytes differs from other European Anura in that its strings of eggs are not laid in the water,[1] but are twisted round the legs of the male and carried for some time during their stages of embryonic development. Their bearer only resorts to the water when they are ready to hatch as advanced tadpoles having a single pair of gills covered by an operculum.

When these animals are kept at a higher temperature (25°—30° C.) with access to water, the eggs are laid in the water, and they hatch earlier, when the gills are still exposed. If these conditions are continued, so that the animals are obliged to breed in the water, by the F_4 generation the tadpoles will have three pairs of gills as in other frogs. A number of other interesting changes occur. The eggs of Alytes are much larger and less numerous than in other frogs and toads. Thus, *Rana* produces 600-4,000 eggs with a diameter of only 1·7 mm, while in Alytes the number of eggs is about 60 and they are 3·5-4 mm. in diameter owing to a great amount of yolk. Developing in the water, the eggs of Alytes become rapidly smaller in successive generations.

But perhaps the most critical of these results concerns the secondary sexual characters of the male. Here again Alytes differs from other Anura in the absence of the characteristic horny pad which developes on the thumb or wrist of the male during the breeding season, enabling him to retain his hold on the female while in the water. When pairing and egg-laying occur in the water, however, according to Kammerer this pad gradually appears in Alytes, until

[1] It is an interesting fact that in one locality, Münster in Westphalia (Kammerer, 1909, p. 452), the eggs are normally laid in water.

by the F_5 generation it is fully developed. This is said to be accompanied by an increase in the musculature of the arms. The development and regeneration of the pad are found to be independent of hormones from the sex organs, since castration of the males does not affect it. Also it is said that when F_2 males in which the patch had partly developed were crossed with normal Alytes females without a patch, a Mendelian result was obtained. This will certainly require additional evidence before it can be accepted.

The fact that in all Anura this pad only becomes apparent during the breeding season, seems to indicate that it is of relatively recent origin and has not become fully established in the germplasm. It is still in the condition of an organismal rather than a nuclear character. Whatever interpretation is put upon these results, as indicating a return to ancestral conditions or otherwise, it seems difficult to escape the conclusion that functional inheritance has taken place in these experiments[1], even if the gradual transition be looked upon as a reversion. Nevertheless, one can scarcely suppose that evolutionary adaptation takes place at any such rapid rate.

It is at any rate an advantage that the subject of inheritance of acquired characters is emerging from neglect into the region of critical experiment, and the attitude with regard to it is becoming less dogmatic and more cautious. Darwin found no difficulty in accepting both the Lamarckian and selection factors as contributory to evolution. We are endeavouring to show that from the point of view of our present knowledge of organic structure the neo-Lamarckian and mutation factors are not incompatible or mutually exclusive.

A recent paper which is of interest because it frankly subsumes the neo-Lamarckian factor (Roberts, 1919), developes the hypothesis that mechanical reaction to stress is the law in all tissues. Just as the flying buttresses of a Gothic cathedral were the result of an effort to shore up walls which were spreading under the increased

[1] MacBride (1919) upholds Kammerer's contention. Bateson (1919) in a reply points out that the fingers in the photograph of the control frog in Kammerer's paper have been clumsily retouched or painted over, and that the critical photograph showing the Brunftschwielen of the modified male shows what appears to be a sort of excrescence on the outside of the fourth finger of the right hand. This, however, does not alter the evidence for the presence of a Brunftschwiele, which is clearly shown in the photograph as a lump on the right wrist. Moreover, a series of nine histological drawings from sections of the horny pad are given, showing the details of structure of this region in males of Alytes in which it is wholly or partly developed, also during the breeding and resting seasons, and in females. These drawings must either be regarded as evidence, in which case they prove Kammerer's point, or treated as deliberate frauds. There seems no sufficient reason for adopting the latter alternative, but it is certainly to be expected that Dr. Kammerer will now be able to produce specimens showing the horny pad.

weight of the roof; so alternate breakdown and repair have led to the present structural relationships in many parts of the human body. Thus the heart is described as an aneurism, and the stomach as a dilatation sac, whose thick muscular wall has developed as the result of disaster and repair. It is assumed that the transmission of these changes probably takes place by a morphogenetic reply *in utero* to increased functional stresses.

Brief mention must be made of the important work of Harrison (1920a) on melanism and other racial characters in certain Geometrid moths. After intensive observation and experiment with the genus Oporabia, Harrison concludes that the subspecies *O. filigrammaria* was evolved from *O. autumnata* during the Glacial period by the action of changed climatic conditions, and that "almost certainly" many of the racial and subspecific differences are "true Lamarckian effects," in particular the food instincts in *O. filigrammaria* and the period of emergence of the pinewood race of *O. autumnata*. Moreover, a Lamarckian explanation of melanism is considered necessary, the darkening resulting from metallic salts in the food, derived from the smoke in industrial areas and from sea fogs in coastal areas where melanism frequently occurs. Melanism is known to behave as a simple Mendelian dominant in many species (see *e.g.*, Onslow, 1920). Harrison (1920b) has recently shown this to be true of the melanic variety of *Tephrosia crepuscularia* when crossed with the type, but in interspecific crosses between *T. crepuscularia* and *T. bistortata* a chaotic series of F_2 and F_3 forms was obtained, the behaviour being no longer describable in Mendelian terms. This recalls the result obtained by the writer (1915f) in crosses between the Mendelian dominant character in *Œnothera rubricalyx* and another species, *Œ. grandiflora*. In both cases dilution and modification of the character has resulted from crossing with a different species. If crossing will modify such a unit-factor, then it is not unreasonable to suppose that they may be capable of environmental modification.

If the Lamarckian explanation of melanism is a true one, then it would appear to be a case of parallel induction, because of its manner of inheritance in crosses, indicating that the nuclear structure is already altered. The function of hormones as an evolutionary means of handing on or accelerating modifications, as suggested by Cunningham (1908), Dendy (1911) and others, indicates a method by which modifications may be perpetuated until the change becomes germinal by producing an alteration in the nucleus.

This is obviously a field where more definite conceptions will only be possible after much further experimental work.

To mention a single case of experimental morphogenesis in plants, Harper (1918) has carefully studied the organization and reproduction of Pediastrum colonies, and concludes that from the point of view of inheritance the characters are of different kinds. The four-lobed shape of the cells of a colony he thinks may be an adaptive character which arose as an environmental response to the pressure relations between cells and has now become fixed and transmitted by cell division.

In the ostrich [1] there are two callosities on the ankle, one median which appears before hatching, hence inherited; the other on the side, which appears only after the bird uses this surface to rest upon and is not transmissible. It is indicated that the median callosity is much older, dating back to the Pliocene ostrich, which, having three toes, rested on its legs symmetrically and so developed the median callosities which have since become inherited independently of any external stimulus. This callosity is no longer used, the loss of the third toe, according to Duerden, having led to a shifting of the point of contact with the ground and the development of a new callosity which is not transmitted. The difference in inheritance of these two callosities is very difficult to explain satisfactorily on any basis except that of functional inheritance.

Brief reference must also be made to two important papers by Guyer and Smith [2] recently received. A fowl serum was prepared sensitized to (*i.e.*, containing a cytolysin which dissolved) the lens of the eye of the rabbit. This serum injected into pregnant rabbits produced inherited defects in the eyes of many of the young. Experiments with mice gave similar results. In rabbits the defects were transmitted for six generations, through the male as well as the female, and were gradually intensified without any further injections. The defect behaved in general as a Mendelian recessive. Here is clearly a specific modification produced by extrinsic factors.

In concluding this chapter, it is evident that conceptions of functional inheritance in various forms are again making themselves felt in much of the constructive thinking of the present time.

[1] Duerden, J. E. Amer. Nat. Vol. 54, 1920.

[2] Journ. Exptl. Zool. Vols. 26, 31.

CHAPTER XI.

General Comparison of Recapitulatory and Karyogenetic Characters.

The Biogenetic Law.

It is only necessary to refer to two recent discussions of the biogenetic law in addition to those already cited. In his excellent book on form and function, Russell (1916) has written a history of animal morphology, including numerous references to the biogenetic law. Those who have opposed the law appear to have based their beliefs largely on (1) the dissimilarities found in related embryos and eggs, (2) the fact that specific characters often make their appearance very early in the ontogeny. Now both these situations are to be anticipated if mutations have taken place in organisms which already display recapitulatory characters. One of the most striking cases of the appearance of specific characters very early in the ontogeny, is cited by Russell (l.c., p. 352), who quotes Louis Agassiz. The latter wrote in 1859 that the snapping turtle "exhibits its small cross-like sternum, its long tail, its ferocious habits, even before it leaves the egg, before it breathes through lungs." It snaps at everything brought near, even when still surrounded by its amnion and allantois. This is to be expected if the specific characters in question have originated through mutations, for it is now well-proven, in plants at least that mutational characters begin to express themselves very early in the ontogeny. And this is a natural result of the circumstance that they are present in every nucleus. On the other hand, there is a certain amount of embryological evidence in animals that characters borne in the nuclei (in contrast to morphogenetic substances in the egg cytoplasm) frequently became actuated only after the earlier cleavage stages are passed. That such characters make their first appearance earlier than some of the recapitulatory characters which they traverse, is also to be expected; but it only limits and does not nullify the biogenetic law, since that law applies only to recapitulatory characters but not to ordinary mutational characters.

Sedgwick's (1894) criticisms of von Baer's law are based on the same objections as those considered above. He compared the embryos of the fowl and dogfish, admitting that they agree in many important points, as the presence in the chick of pharyngeal clefts, a tubular piscine heart, a similar arrangement of the cardiac

arterial system, a cartilaginous endo-skeleton, oro-nasal grooves and a notochord. But he finds "equally important differences." Nevertheless, he admits the essential point for recapitulation—that embryos pass through "stages of structure permanent in lower members of the same group." He also says (p. 43), "The evidence seems to indicate that in a number of cases adult variations of any part are accompanied by precedent similar alteration of the same part in the embryo." We have already seen that this is accounted for on a mutational basis.

It is well-known that Hyatt showed with fossil Ammonites that there is recapitulation in successive coils of the shell, the first coils often reproducing characters belonging to types known from the palæontological record to be ancestral. His law of acceleration in development, deduced from purely palæontological observations is simply another expression of the more recent embryological law of tachygenesis.

Morgan (1916, p. 19) has recently expressed the view that the new mutationist ideas have played havoc with the biogenetic law. He says, for example, that the chick, the fish, and man all possess gill-slits at an early stage of their development merely because they have not lost them. But this merely glosses over a difficulty without explaining it. The fallacy in such an explanation is evident enough if one applies it to such a recent recapitulation as that of the parasitic Copepod, Achtheres (see page 232). In such a case the *larval* stage of this copepod corresponds obviously to the *adult* stage of free-living copepods. Achtheres, however, passes through and beyond this stage, and *its* adult stage has lost practically all its copepod features. We venture to think this is a recapitulatory phenomenon, involving a lengthening of the life-cycle and probably also the inheritance of acquired characters.

Relation to Geographic Distribution.

Brief allusion only will be made to this subject. We have already seen that recapitulatory characters appear to involve a gradual adaptation to a new habitat, while mutations do not. In this connection we have pointed out (Gates, 1917c) another relationship between variation and geographic distribution. With reference particularly to North American owls (*Otus asio*), it was shown that in Eastern North America the red colour phase, which occurs usually in the same regions as the gray with which it interbreeds, probably originated as a mutation and behaves as a dominant Mendelian character. In Western America, on the other hand, a

series of geographic sub-species succeed each other down the Pacific coast, the most northern form being largest and with dark brown markings, while further south they become progressively smaller and lighter in colour, *i.e.*, with less brown and more gray. These various sub-species are co-terminous with each other in their distribution and they form a very close, practically continuous series. The conclusion was reached that while such discontinuous variations as the red colour phase are independent of environmental or functional influence, the continuous type occupying distinct and adjacent geographic areas, represents the results of the stress of environment on the species in its dispersal, leading to the gradual differentiation of local races or sub-species.

Sumner (1918), in his studies of the deer mice, *Peromyscus maniculatus*, has arrived at similar conclusions regarding the occurrence of both mutations and gradual differentiations, and their geographic relationships. This subject is one which requires much further investigation, but it is at least possible that this continuous type of geographic variety in its origin involves the neo-Lamarckian factor.

The neo-Lamarckian principle.

Experiments have shown that impressed modifications may affect the offspring for at least two generations, and to this extent the neo-Lamarckian principle has already been justified. The mechanism of transmission in such a case is apparently different from that of a mutation or a Mendelian character in a cross. The latter appears to be determined in the nuclei, and therefore transmitted as a stable and permanent feature. The acquired character is temporary, cytoplasmic in origin, and will not be permanently retained unless re-impressed generation after generation until the nuclei of the germ cells are ultimately altered in their constitution.

The fixation of such an organismal character may require a longer or shorter number of generations. What determines the number of generations required is quite unknown at the present time, nor is the *modus operandi* understood. But we may assume that in the process, altered metabolic products in the cytoplasm ultimately produce a modification of a chromatin element which is permanent in character. It may be expected that such a transformation will occur much more rapidly in some cases than others.

The views here set forth regarding the occurrence of both mutational and adaptational characters in organisms are entirely in harmony with Dendy's (1913, 1916) conclusions from investigations of the sponges. He concludes that the specific characters of sponges are generally non-adaptive, and that a great many of the spicule differences so characteristic of the group must have originated by mutations. He also points out what we would now regard as parallel mutations, as in the appearance of trichodragmata, and in the polyphyletic family Epipolasidæ, which is an assemblage of stelletid sponges which have independently lost their triæne spicules. Usually the most minute differences, both in megascleres and microscleres, remain constant throughout the species, though millions of spicules may occur in each individual, to whom these microscopic differences cannot be of the slightest use. Such differences point to chemical or physical alterations in the constitution of the germplasm.

On the other hand, adaptive modifications of spicules for various purposes have taken place, as in the modification of triænes into grapnels for anchoring the sponge to a muddy bottom, or into discotriænes which serve as a dermal protection. Some of these adaptive conditions may have come about through selection among a series of mutations, but it is difficult to see that any of them involve the principle of inheritance of acquired characters.

CHAPTER XII.

Orthogenetic Characters.

In previous chapters we have drawn a contrast between (a) karyogenetic characters originating as mutations in the germplasm and affecting every nucleus, and (b) organismal characters which belong to the organism as a whole, show recapitulation, and probably originate as environmentally impressed modifications of the cytoplasm. In this chapter we wish to consider briefly orthogenetic characters, which appear to stand midway between these two categories. Like the former they are germinal in origin, and like the latter they show recapitulation. But they differ from the recapitulatory characters previously considered, in that their origin is apparently not adaptational but on the contrary independent of environment. We will refer only to three cases from the recent experimental work with animals.

It is a well-known fact that in many birds the juvenile plumage differs from that of the adult, and usually at least represents a less specialized and presumably ancestral type of plumage. One of the most striking cases, recently studied by Beebe (1914), is in the white ibis, *Guara alba*. In the young chick the head and neck are covered with black down, becoming smoky gray over the greater part of the body except the under parts, which are white. In the juvenile and post-juvenile stages this is gradually replaced by white feathers, until late in the second year the birds are pure white with scarlet legs and bill. It seems clear that such a white bird has not originated through a mutation, and that the ontogeny represents a gradual transition from a dark-coloured ancestor. It is an interesting fact that the white loral spots in the young chick, which quickly disappear, apparently represent the permanent facial marking of a related ibis, *Plegadis autumnalis*. This would appear to be one of the few cases in which a specific (generic) difference is at the same time a recapitulatory character.

Whitman's (1919) recent posthumous volumes on orthogenetic evolution in pigeons cite a number of cases of juvenile plumage as recapitulatory stages furnishing evidence of orthogenetic development. Whitman's study of the wing patterns of pigeons is perhaps the most prolonged and intimate investigation which has ever been made of a single character. Reading the series in the opposite direction from Darwin, he concluded that the primitive condition was a uniform chequered pattern covering the whole wing, as in

the Japanese turtle dove. Then he shows how in different groups of wild species of pigeons from all over the world, various stages of the reduction of this pattern are found, beginning always at the anterior end of the wing and wiping off the rows of spots until, in unrelated species belonging to different groups, patterns with 4, 3, 2, 1 or no bars of spots may be found. The rock pigeon *(Columba livia)* with usually two wing-bars thus represents a relatively reduced condition, while the white-winged pigeon (*Melopelia leucoptera*), in which the chequers have entirely disappeared, is a still more advanced stage. In these cases, moreover, the juvenile plumage generally represents the more extensively chequered and primitive type, recapitulation thus strongly supporting the author's interpretation. Whitman further claims that this orthogenetic trend in the colour patterns of pigeons is not a mere result of selection, but may even run counter to it and gradually eliminate a pattern of spots which sexual selection tended to strengthen and beautify. His monumental work places in a new light the claims of orthogenesis as an evolutionary factor, but space forbids a more extensive discussion of his results.

The claims of orthogenesis have also been taken up recently by Duerden (1919) for the ostriches. He believes that the reduction in the plumage, in the toes and their scutellation, and in other features, is proceeding progressively and independently in the North and South African ostrich. He believes the evidence is clear that the progress is entirely independent of adaptational considerations. On the other hand, there seems no doubt of the germinal origin of many of the variations. The case of reduction in toes and specialization of the middle toe for running is in many respects similar to that of the horse. If that is so, adaptation would appear to have taken place by the progressive selection of germinal variations. It does not necessarily follow, as Duerden believes, that the reduction of the ostrich's toes will continue until the extinction of the species results.

The last five chapters have been devoted to an attempt to bring into relation with each other such diverse things as the mutation theory, the cell theory, the facts of recapitulation and the evidence for the inheritance of acquired characters. We found that new features of the organism may originate internally through chromatin changes and express themselves centrifugally in the ontogeny of the organism; or they may originate externally as organismal characters and ultimately become inherited, through a

centripetal effect on the nuclei. We also concluded that karyogenetic characters were not as a rule recapitulatory, because they imply a change in the nuclear unit which is transmitted by mitosis to every cell, while organismal characters may become so by adding on certain stages to the life-cycle of the organism. The existence of these two types of characters accounts for many anomalies in the biogenetic law. The existence of two such classes of characters makes it possible to understand better many features of organic structure and inheritance.

But it is obvious that the relationship between these two types of characters cannot be fully understood in all their aspects at the present time, nor can a sharp line always be drawn between karyogenetic, cytogenetic and orthogenetic characters—in some aspects they shade into each other. As a constructive attempt to harmonize two bodies of evidence which are obviously in conflict and have long been considered irreconcilable, we make no apology for its tentative character and incompleteness.

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NOTES ON FRESHWATER ALGÆ. I—IV.

By W. J. Hodgetts, M.Sc. (Lond.)

[With Two Figures in the Text.]

I.—A New Species of *Pyramimonas*.

During April and May, 1920, a small motile Alga belonging to the genus *Pyramimonas* (family Polyblepharidaceæ of the order Volvocales) was observed in fair quantity among filaments of *Spirogyra* and *Tribonema* in the overflow ditch of a small pond at Quinton, near Birmingham. The Alga appeared to be absent from the pond itself, occurring only in the very shallow water of the ditch, into which, owing to the heavy rains of April, water from the pond had run. The water of the ditch in places was coloured light green owing to the presence of this Alga. On keeping specimens in the laboratory in open tubes and wide-mouthed glass jars the organism always became encysted after 24-36 hours, and eventually died; and attempts to cultivate it in dilute nutrient solutions were also unsuccessful.

The form of the motile cell is very variable, the commonest shape being sub-pyramidal (Fig. 1, A), sharply truncate and slightly 4-lobed at the anterior end, and somewhat tapering towards the posterior extremity. Transitions to shorter forms which are more or less cordate (Fig. 1, B), or even sub-globose were frequent; while on the other hand more elongated sub-cylindrical individuals (Fig. 1, C) were not rare. The widely truncate anterior end is a characteristic feature of all the cells, and when the latter are observed in anterior view this end is sub-quadrate with rounded angles (Fig. 1, D), due to the four anterior lobes. The usual number of these lobes was four, but occasionally only three were seen in anterior view, giving a sub-triangular form to this end of the cell. The anterior lobes are strictly confined to the anterior end of the cell, and are not continued backwards as ridges, or at any rate are continued for only a very short distance, so that the (optical) transverse section for the greater part of the length of the cell is circular. There is a well-marked depression in the centre of the anterior end, and from the base of this depression arise four cilia.

The motion of the cell is always cilia-end foremost, while at the same time the cell rotates about its longitudinal axis in a direction which (the cell being considered as swimming towards the observer) is clockwise.

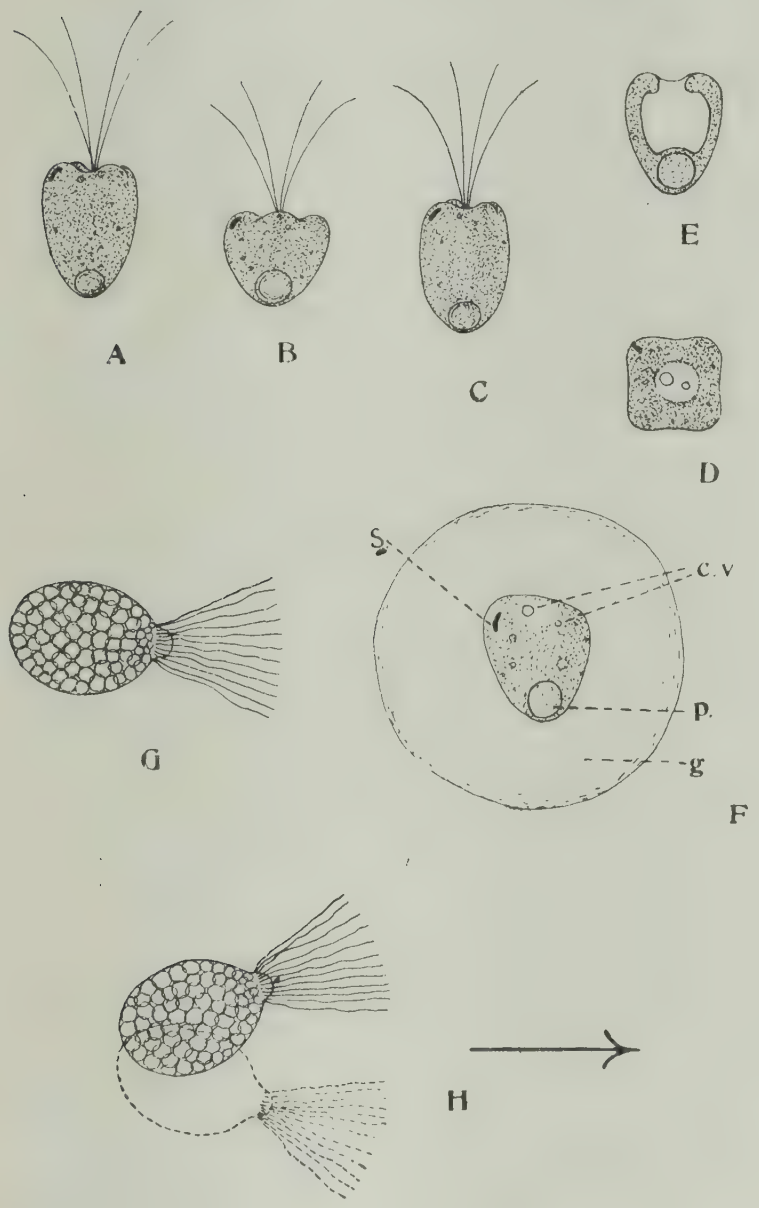


FIG. 1, A—H.

A—C. *Pyramimonas inconstans* sp. n. Various forms of vegetative individuals.

D. Anterior view of motile cell of *P. inconstans*, showing sub-quadrate form, stigma and the two contractile vacuoles (the cilia are not shown).

E. Optical longitudinal section of *P. inconstans*, showing the form of the chloroplast in long. sect., and the basal pyrenoid.

F. Non-motile individual of *P. inconstans*; s. stigma, c.v. the two contractile vacuoles, p. pyrenoid, g. thick hyaline gelatinous investment.

G. Zoogonidium of *Oedogonium cryptoporum*, killed with a drop of dilute iodine solution.

H. Diagram illustrating mode of progression of the zoogonidium of *O. cryptoporum* (described in text).

A—F × 1250; G, H × 900.

There is no cellulose cell-well, the cell being covered with a very delicate protoplasmic membrane, which appears to allow of a certain amount of change of form of the cell. Although such alteration in form was not directly observed in the motile individuals, yet the variability in the shape of the cells seems to be due in part to this power. In the non-motile state, as described below, the cells readily assume various forms, although they generally tend to become sub-globose.

There is a single cup-shaped, bright green chloroplast, occupying practically the whole periphery of the cell, leaving only the centre of the anterior end free and more or less hyaline. The anterior edge of the chloroplast is incurved and slightly thickened, as shown in the optical longitudinal section, Fig. 1, E, while the thickened base of the chloroplast contains a large conspicuous pyrenoid. A rather pale red stigma of elongated form is situated on the outer surface of the chloroplast in the anterior part of the cell, and invariably on the summit of one of the anterior lobes (Fig. 1, A—D), and projecting slightly above the general surface of the cell.

The chloroplast appears to be quite entire at the anterior end. Even under very high powers (a 2 mm. oil-immersion objective was most frequently used in examining the minute structure of the cell), and in cells blistered with a drop of dilute formalin solution, or killed with iodine, or other reagents, the incurved anterior edge of the chloroplast never appeared to be divided into lobes corresponding to the four anterior lobes of the cell.

The pyrenoid has a starch sheath, and minute grains of starch were frequently observed scattered throughout the chloroplast. The addition of a drop of dilute formalin solution causes the cells to become greatly swollen and distorted in the same way as that described by B. M. Griffiths in the case of *Pyramimonas delicatulus*.[1]

Within the chloroplast and in the general cytoplasm of the anterior region of the cell are two (occasionally three) contractile vacuoles. They are very difficult to observe in moving individuals, although occasional glimpses of one or both of them can be obtained. They are more readily seen in the non-motile cells (Fig. 1, F), especially under a high magnification. The period between two successive disappearances of a vacuole is 18—22 seconds. Other small vacuoles were observed in different parts of the cell but these were never observed to pulsate.

[1] B. M. Griffiths. On Two New Members of the Volvocaceæ, New Phytol., VIII, 1909, pp. 130—137.

Under unfavourable conditions the organism readily assumes the "*Palmella*"-state. The cilia are lost and the cells assume various irregular shapes, but generally tend to become more or less sub-globose, the anterior lobes become usually unrecognisable, and the outlines of the chloroplast very indistinct, although stigma and pyrenoid persist, and the contractile vacuoles become more apparent (Fig. 1, F). Around each cell there develops a thick hyaline gelatinous investment (g in Fig. 1, F), and numerous cells often become aggregated together in a common jelly.

These non-motile cells can undergo slow change of form. Griffiths (l.c. p. 134) states that no amœboid alterations in the shape of the cell was observed in *P. delicatulus*, and further remarks that "in this respect *Pyramimonas* appears to differ from the other members of the Polyblepharidaceæ." West,[1] writing of the Polyblepharidaceæ, states that "the body of the cell is invested only by a protoplasmic membrane and, with the possible exception of *Pyramimonas*, is able within prescribed limits to undergo certain changes of form." These two statements concerning *Pyramimonas* are, however, true only in the case of *P. delicatulus*, since Dill in his account of *P. tetrarhynchus* (the third known member of the genus) says "Während der Bewegung sowohl als in der Ruhe konnte ich an diesen Organismen Formveränderungen wahrnehmen."[2] Dill also quotes Dangeard (Le Botaniste 1889, p. 138) as having observed alteration of form ("metabolie") in *P. tetrarhynchus*.

Division of the cell is longitudinal, and takes place in motile as well as non-motile (encysted) individuals, the process of division resembling that described by Griffiths in the case of *P. delicatulus*. It commences at the posterior end of the cell, and gradually extends anteriorly. In the case of motile cells the cilia increase in number to eight prior to cell-division, each daughter cell retaining four.

This species (termed *P. inconstans* on account of the variability in form of the cell) differs from both *P. tetrarhynchus* Schmarda[3] and *P. delicatulus* Griffiths (l. c.) in the smaller size of its cells, the non-lobed chloroplast, and the anterior stigma. From the last-named species it further differs in having no posterior excavation in the chloroplast. The anterior lobes of the cells of *P. inconstans* are also much less developed than those of

[1] West, G. S., Algæ, Vol. I. Camb. Univ. Press, 1916, p. 164.

[2] Dill, O. E., Jahrb. f. wiss. Bot., XXVIII. 1895, p. 344.

[3] Described by Dill, l. c.

either of the other two species. Altogether the cell-structure of the present species is simpler than that of the other two, and for this reason *P. inconstans*, may perhaps be considered as a link connecting these with *Polyblepharis*, which is generally considered as the most primitive genus of the family Polyblepharidaceæ.

The conditions which seem to favour the development of the motile state of *P. inconstans* in nature appear to be (1) relatively dilute pond water, (2) a moderate temperature (about 8°—13° C), and (3) abundant aeration of the water. The last factor seems important when it is considered that the water of the ditch was renewed after each shower by water overflowing from the pond (itself much swollen with rain-water); and also from the fact that motile individuals in a drop of water under a cover-glass all lost their motility in about two hours (probably owing to scarcity of oxygen), while a species of *Chlamydomonus* in the same drop of water was observed to retain its motility for a much longer period.

PYRAMIMONAS INCONSTANS sp. nov. Cellulæ parvæ, plerumque subpyramidatæ sed nonnunquam cordatæ vel subcylindraceæ, polo anteriore late truncato et leviter quadri-lobulato, a vertice visæ subquadratæ (interdum subtriangulæ); chromatophora singularis, viridis, parte anteriore incurvata sed non-lobulata, pyrenoide singulo posteriore instructa; stigma elongatum, in parte anteriore cellulæ situm; vacuolæ contractiles binæ (interdum ternæ).

Long. cell. (8·8)—10—15μ,
lat. cell. 7·5—10μ,
long. ciliorum 13—18μ.

Hab. in fossa, Quinton, prope Birmingham (April and May, 1920).

II. Note on the Zoogonidia of *Oedogonium cryptoporum*.

Some observations were made in March 1919, on the zoogonidia of *Oedogonium cryptoporum*, obtained from Bearwood, near Birmingham. Vegetative specimens of the Alga brought into the laboratory and placed in a large glass vessel of pond water proceeded to form zoogonidia in very large numbers. No mature oogonia were present at that time but later in the spring they matured, and the species was identified as *O. cryptoporum*, Wittr., the record being confirmed by the late Professor G. S. West.

The interesting point about the zoogonidia, hundreds of which were examined, was the length of the cilia. All standard works on freshwater Allgæ appear to agree in describing and figuring the zoogonidia (and also the androgonidia and spermatozoid) of

Oedogonium a having as crown of relatively *short* cilia. Published figures generally show the cilia about $\frac{1}{8}$ to $\frac{1}{4}$ as long as the body of the zoogonidium. The length of the cilia of the zoogonidia of *O. cryptoporum* (Fig 1, G), however, were observed to be $\frac{2}{3}$ to $\frac{4}{5}$ of the body-length, as the measurements given below show.

The zoogonidium of *O. cryptoporum* is oval or subellipsoid in shape, with a prominent hemispherical and hyaline anterior papilla. Fig. 1, G shows the position the cilia always assume when the zoogonidia are killed with a drop of dilute iodine solution. The following are a few measurements of the length of cilia and length of body of the zoogonidium (including the anterior papilla).

Body-length	22·5	20·0	19·7	20·0	21·5	20·0μ
Length of Cilia	15·8	15·5	14·0	16·0	15·5	15·2μ

The relative length of these cilia appears to be markedly greater than that recorded in the motile cells of any other member of the Oedogoniales, as far as can be ascertained from published figures.

The zoogonidia of this species have no eye-spot and are negatively phototactic, always accumulating on the side of the culture-vessel which is turned away from the source of light.

The mode of progression is rather interesting and is represented by Fig 1, H. The arrow gives the general direction in which the zoogonidium is moving, but the longitudinal axis of the latter is never parallel to this direction but makes an angle of about 22·5° with it. Observed under a low magnification the anterior end of the moving zoogonidium appears to oscillate from side to side, but in reality the anterior end describes a circle, the direction of its motion (the zoogonidium being considered as moving towards the observer) being anti-clockwise. In other words the longitudinal axis of the zoogonidium describes a cone, the apex of which is the extreme posterior end of the zoogonidium while the axis of the cone gives the actual direction in which the zoogonidium is moving as a whole.

Occasional zoogonidia of several other (undetermined) species of *Oedogonium* and *Bulbochæte* have been seen at various times, but the relative length of their cilia was always observed to be very much shorter than is the case with those of *O. cryptoporum*. Doubtless, however, this species does not stand alone in having zoogonidia with rather long cilia.

III.—On the Occurrence of "False-branching" in the *Hormidium*-state of *Prasiola crispa*.

As is well-known, the cells of the common filamentous form, or *Hormidium*-state, of *Prasiola crispa* frequently divide by longitudinal as well as transverse walls to form two or more rows of cells (*Schizogonium*-state), which by further divisions produce flat expansions of cells (*Prasiola*-state). True branching in the *Hormidium*-state of this Alga appears to have been recorded only in connection with the production of rhizoids. Wille, for example has described a submarine form of *Prasiola crispa* (termed f. *submarina*[1]) in which certain cells of the filaments had grown out to produce short unicellular rhizoids; only very occasionally did these rhizoidal branches consist of several cells.

Choldat[2] mentions and figures uni- and multi-cellular, simple and also branched, rhizoids in *Schizogonium crispum* (=*Prasiola crispa*). Heering,[3] speaking of the rhizoids of *Prasiola* says: "Selton werden diese Ausstülpungen durch eine Scheidewand von der Mutterzelle abgegrenzt und wachsen zu mehrzelligen Fäden aus."

The writer, however, found pseudo-branching of a character quite different from rhizoid-production in a patch of the *Hormidium*-state of *Prasiola crispa* which occurred on damp ground under a tree in a field at Warley, near Birmingham (in April, 1919). As will be seen from the description below, this pseudo-branching is exactly similar as regards mode of development to the false-branching in the Blue-green algal genera *Tolypothrix* and *Scytonema*.

The mode of development of these pseudo-branches, which were quite frequent and not merely of isolated occurrence in specimens of the Alga from the locality mentioned, is illustrated in Fig. 2, A-D. At intervals along most of the filaments there were short lengths of 1 to 3 (rarely more) dead, apparently empty, and generally much flattened cells (Fig. 2, A).

The living cells on one or both sides of these dead cells, by active division and growth had, in the case of many filaments, pushed their way out through the hyaline sheath surrounding the filament (Fig. 2, B, C.) as short lateral pseudo-branches (Fig. 2, D).

[1] Wille, N., Studien über Chlorophyceen, III, Vid.-Selsk. Skrifter. I. Math.-naturv. Klasse, 1900 (Christiania), pp. 13-18, Taf. 1, Figs. 42-53.

[2] Algues Vertes de la Suisse, Berne, 1902, p. 342, and Fig. 251.

[3] Heering, W., Die Süsswasserflora Deutschlands, Heft. VI, 1914 (Jena), p. 56.

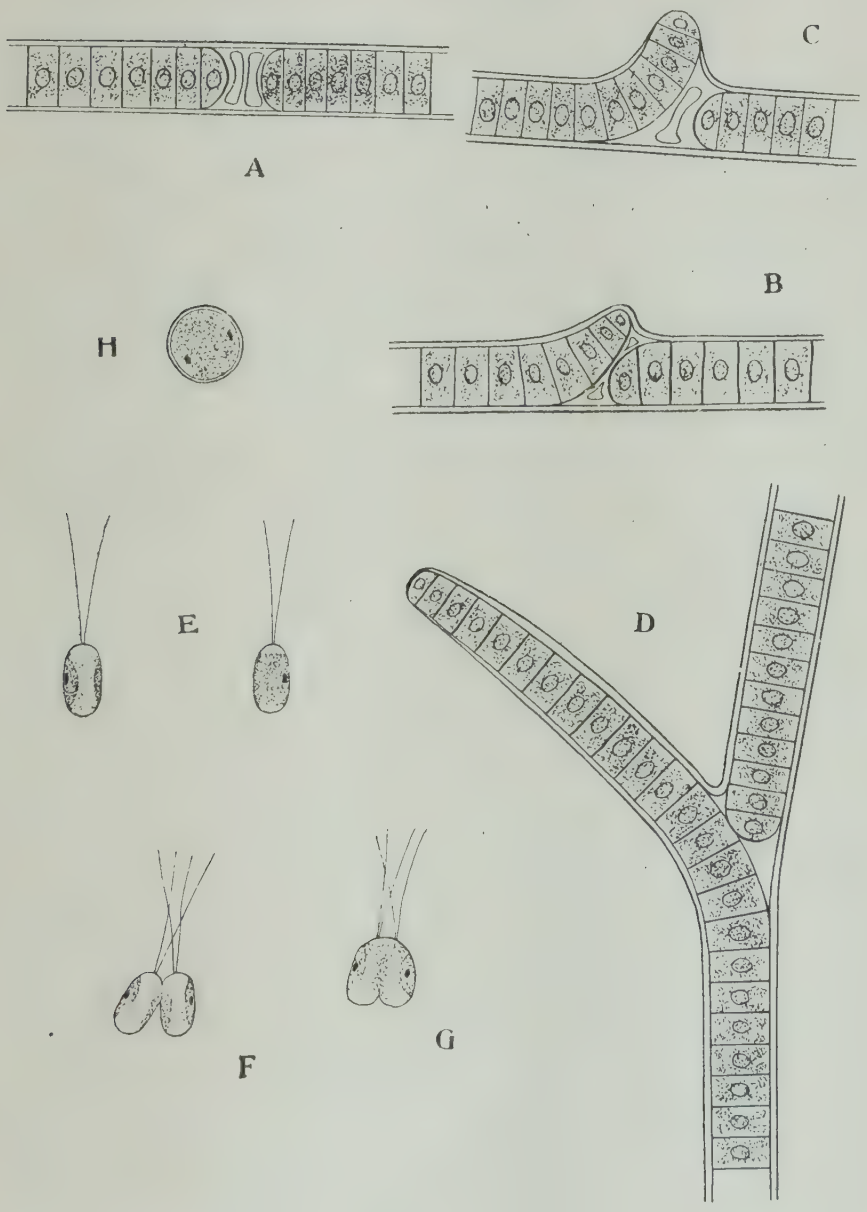


FIG. 2, A—H

A—D *Prasiola crispa*, showing mode of development of pseudo-branches.
A. Two dead and shrivelled cells in a filament.
B, C. Very young pseudo-branches.
D. Older pseudo-branch.
E. Gametes of *Chlamydomonas variabilis* Dang., showing the form of the chloroplast.
F. The same just beginning to fuse.
G. Later stage in process of fusion of the gametes.
H. Zygote, showing the two persistent stigmas.
A—D × 550; E—H × 800.

The dead intercalary cells which were generally present at the point in the filament where the false-branches arose, are thus curiously analogous to the heterocysts of *Tolypothrix* and *Scytonema*, in the relation which they bear to the false-branches. The closest resemblance is to *Tolypothrix*, where the pseudo-branches arise singly and the heterocysts are seriate; occasionally, however, in the *Prasiola* the pseudo-branches arose in pairs, one on each side of the dead intercalary cells, thus recalling *Scytonema*.

Several writers have described the occurrence of dead, flattened or biconcave, cells in filaments of the *Hormidium*-state of *Prasiola crispa*. F. E. Fritsch,[1] for example, described and figured such dead cells in specimens of the Alga from the Antarctic, and the dead cells mentioned above in the Warley material appear to be similar to those described by this author.

Occasionally no sign of dead intercalary cells could be seen at the point of origin of the pseudo-branch, and in several cases it was distinctly seen that the latter was given off at a place in the filament where no dead cells were present. Possibly the development of these pseudo-branches in *Prasiola* may be explained by the Alga having gone through a short period unfavourable to growth, which resulted in certain intercalary cells being killed, and their contents disorganised,[2] while, favourable conditions again ensuing, the filaments later resumed active growth and produced the pseudo-branches at places of weakness in the filaments.

The apices of the pseudo-branches always consisted of somewhat narrower and thinner-walled cells, obviously in process of active division and growth. The "branches" were generally short (rarely more than 25 cells in length) but doubtless given favourable conditions they might have grown much longer.

Examination of *Prasiola crispa* from other localities, and at different times, has resulted in the finding of only isolated examples of this false-branching. It seems that the conditions required to produce the pseudo-branches in abundance are only locally or occasionally realised, so that their production is perhaps to be looked upon as a somewhat abnormal phenomenon.

IV.—Sexual Reproduction of *Chlamydomonas variabilis*.

The gametes of this species of *Chlamydomonas* do not appear to have been hitherto observed, or at any rate described. Wille

[1] Freshw. Algæ in Nat. Hist. Report, Brit. Antarctic Exped., 1910, Bot. Pt. 1, 1917.

[2] Or these cells may have been killed by some parasite.

[3] Wille, N., Algolog. Notizen, XI. Über die Gattung Chlamydomonas, Nyt Mag. f. Naturv. XLI, 1903, pp. 109-162.

in his monograph of the genus says, under *Chloromonas* (*Chlamydomonas*) *variabilis*, "Gameten? Zygote?"

Chlamydomonas variabilis Dang. has been found by the writer several times in the Midlands, and was very abundant and produced numerous gametes in a small temporary pond in a meadow at Quinton, Birmingham, during February, 1918. The characters of the vegetative cells agreed very well with Wille's description of the species, the form being more or less cylindrical, with a small anterior wart, and the chloroplast a parietal band not quite extending either to the posterior or to the anterior extremities of the cell, so that a small hyaline space was left at both ends of the cell. No pyrenoid was present, but numerous minute starch grains were scattered throughout the chloroplast. The stigma was in the posterior third of the cell. The plane of the first division of the cell was exactly transverse.

The first specimen taken from the pond showed that numerous gametes, many in process of fusion, were being produced (Fig. 2, E). The gametes are isogamous and much smaller in size than the vegetative cells. Size of gametes 8—10μ by 4·5—5μ (the vegetative cells were 15—22μ by 8—10μ).

Morphologically the gametes resemble the vegetative cells, except that the stigma is located nearer the middle of the cell. They have no cellulose wall, being clothed only with a very thin protoplasmic membrane. Eight gametes are produced by each mother-cell. Fusion commences at the anterior ends of the two gametes and gradually extends posteriorly (Fig. 2, F, G.) Partially fused pairs of gametes are still actively motile, and even when completely fused, so long as the cilia are retained, the zygote (zygozoospore) is still motile. The four cilia of each zygote, however, are soon lost and a thin cell-wall secreted (Fig. 2, H). The two stigmas persist for quite a long time in the walled zygospore, but, as the contents of the latter become more granular, they gradually disappear.

Zygospores were produced in hundreds and settled on the bottom of the wide-mouthed glass-jar into which the Alga had been placed. Some weeks after being formed numerous oil-globules appeared in the zygospores, the starch-grains gradually disappearing. The zygospore-wall remained smooth and colourless, and of moderate thickness. Width of mature zygospore 9—12μ. Their germination has not been observed.

PLANT FAMILIES:
A PLEA FOR AN INTERNATIONAL SEQUENCE.

By Alfred Gundersen.

AN almost endless variety of systems and modifications of systems of plant classification have been proposed. While the growth of knowledge demands constant revision, more urgent practical purposes require stability. The formation of a natural classification has become the task of morphology and paleobotany, almost entirely separate from systematic botany. The ideal system of the future must exhibit the course of plant evolution, but the establishment of this exact course is distant. Must meanwhile the confusion from a multiplicity of systems continue indefinitely?

Some Recent Systems.

The Engler-Gilg classification (1912) of the higher plant is:

EMBRYOPHYTA ASIPHONOGAMA.

1. Bryophyta.

2. Pteridophyta (Filicales, *Sphenophyllales*, Equisetales, Lycopodiales, Psilotales, Isoetales, *Cycadofilices*).

EMBRYOPHYTA SIPHONOGAMA.

1. Gymnospermæ (*Cordaitales*, *Bennettitales*, Cycadales, Ginkgoales, Coniferæ, Gnetales).

2. Angiospermæ (Monocotyledoneæ, Dicotyledonæ).

The apparently distinct line separating clubmosses and horsetails on the one hand (Lycopsida) from ferns and seed plants on the other (Pteropsida) was pointed out by Jeffrey in 1898. Scott (1909) considers the construction of the pedigree of the vegetable kingdom to be a pious desire, which will certainly not be realized in our time. To Jeffrey's groups he adds Sphenopsida, thus:

SPHENOPSIDA (Equisetales, *Pseudoborniales*, *Sphenophyllales*, Psilotales).

LYCOPSIDA (Lycopodiales).

PTEROPSIDA (Filicales, *Pteridospermæ*, Gymnospermæ, Angiospermæ).

Bessey (1914) adopts six main groups of vascular plants:

PTERIDOPHYTA (Eusporangiatæ, Leptosporangiatæ).

CALAMOPHYTA (*Sphenophyllineæ*, Equisetineæ, *Calamarineæ*).

LEPIDOPHYTA (Lycopodineæ, *Lepidodendrineæ*).

CYCADOPHYTA (*Pteridospermæ*, Cycadineæ, *Bennettineæ*, *Cordaitineæ*).

STROBILOPHYTA (Pinoideæ).

ANTHOPHYTA (Alternifoliæ, Oppositifoliæ).

According to Berry (1917) the practice of considering Angiosperms and Gymnosperms as sub-classes of the class Exogens was a no more pernicious mask of their true relations than the current usage which separates vascular plants into Pteridophyta and Spermophyta. He proposes seven groups: Angiospermophyta, Coniferophyta, Cycadophyta, Pteridospermophyta, Lepidophyta, Arthrophyta and Pteridophyta.

Conard recently (1919) urges that it is no longer possible to discuss the relationships of plants in the terminology of currently accepted classification, that systematic botany is in immediate need of revision along major lines, and proposes a dichotomous arrangement:

THALLOPHYTA.
EMBRYOPHYTA.
ATRACHEATA or Bryophyta.
TRACHEATA or Vasculares.
Lycopsida.
Pteropsida (Aspermæ or Ferns, Gymnospermæ and Angiospermæ).

Uniform Families by Agreement.

Slightly varying interpretations of the significance of characters, with corresponding variation in nomenclature, makes otherwise similar systems appear very different. In the past names now forgotten such as Phanerocotyledons, Acramphibrya, Rhizogens were given with a view to correspondence with other groups supposed to be co-ordinate. Agreement as to such main groups, even if obtainable, would have no important significance. Smaller groups have had a much greater stability. Ranunculaceæ, Papaveraceæ and numerous other family names are more than a century old.

The number of families of vascular plants is generally considered as about 300. For a number no greater, might not agreement be possible, agreement for a given period not only as to scope but as to sequence? A family sequence, as compared with a complete system of classification would have practical advantages. First, being as to many questions *colorless* it would be more suitable for wide agreement, for the main groups may be variously named and arranged without affecting family sequence. Second, *revision* would mean mainly a rearrangement of sequence without the introduction of new names. Thus successive lists might have a considerable degree of continuity.

"Zoological and botanical systems," says a recent historian of biology, Miall, "owe comparatively little to individual lawgivers; they have been built up piecemeal by the incessant proposal of amendments, and the retention of such as proved satisfactory in practice . . . . . the discoveries, even of great men, have often been vitiated by serious mistakes, which have subsequently been corrected by men of far inferior power." The systems of the future, it seems inevitable, must more and more represent a general botanical synthesis rather than personal views.

Effective international agreements have been reached in a number of sciences. The confusion due to differing opinions as to the atomic weights of the elements was remedied by the establishment of an international list, in this case issued annually. It is of special interest that there is one list only, not many conflicting ones, and that it *bears the name of no individual or institution.* In astronomy the completion of the great international map of the sky depended on many agreements, in particular on a method of *dividing* the subject along definite lines recognized by all. Slightly varying systems of co-ordinates would have rendered international co-operation impossible.

Numbers as Part of Symbols for Families.

Whatever form of classification be used, many publications in all parts of the world require some *linear* sequence of families. A linear sequence is expressed by numbers. Was not the persistence of the Linnaean system in part due to its numerical clearness? "My system is but a tread of Ariadne," said Linnaeus, "a natural system is the first and last aim of systematic botany." Numbers are generally used in arranging genera and species. Dalla-Torre and Harms numbered genera have served in the arrangement of great herbaria. Numbered families have also been used in many publications and might have much wider uses. The somewhat complicated arrangement of the *Natürliche Pflanzenfamilien* into *Abteilungen* and *Teile* was much simplified in the *Pflanzenreich* by the adoption of family numbers assigned in advance, from IV-1 *Cycadaceæ* to IV-280 *Compositæ*. In Forbes and Hemsley's Index Floræ Sinensis family numbers are given *on every page.*

In the International Scientific Catalogue titles are classified by a system of numbers printed near the margin. These numbers at the same time *co-ordinate* the successive volumes. Thus articles on Gymnosperms are found by marginal number 6300 in any

volume. The precise assignment of these numbers is a matter of secondary importance in comparison with the advantages which come from their use.

Standard family numbers if established as a result of general consideration, thus dividing the world of plants along definite lines easily designated, might have various uses, for example :—

(*a*) They would be likely to give direction to morphological investigations.

(*b*) If lists of plants growing in many different parts of the world had the degree of unity implied by uniform family numbers, they would to a much greater degree than at present form a part of one work: the flora of the earth. Such lists would tend towards greater uniformity of nomenclature.

(*c*) Perhaps the time is yet distant when descriptive floras throughout the world may be arranged by a single system. Should it come the solution of numerous questions as to characters and distribution could not but be facilitated.

(*d*) Seed lists of botanic gardens, issued annually, are now arranged by a dozen different methods. Uniformity even among a few gardens would simplify exchanges and would naturally lead to increased co-operation.

(*e*) Botanical gardens cannot cultivate all plants, but wish to know: what are the plants of the world of greatest horticultural, economic or scientific interest? Uniformly arranged planting lists would tend in the direction of an answer, simplifying the work and increasing the value of collections.

(*f*) In the arrangement of numerous herbaria and other collections, especially smaller ones, such as those connected with instruction, where it is desirable that the arrangement should not be too distant from current views.

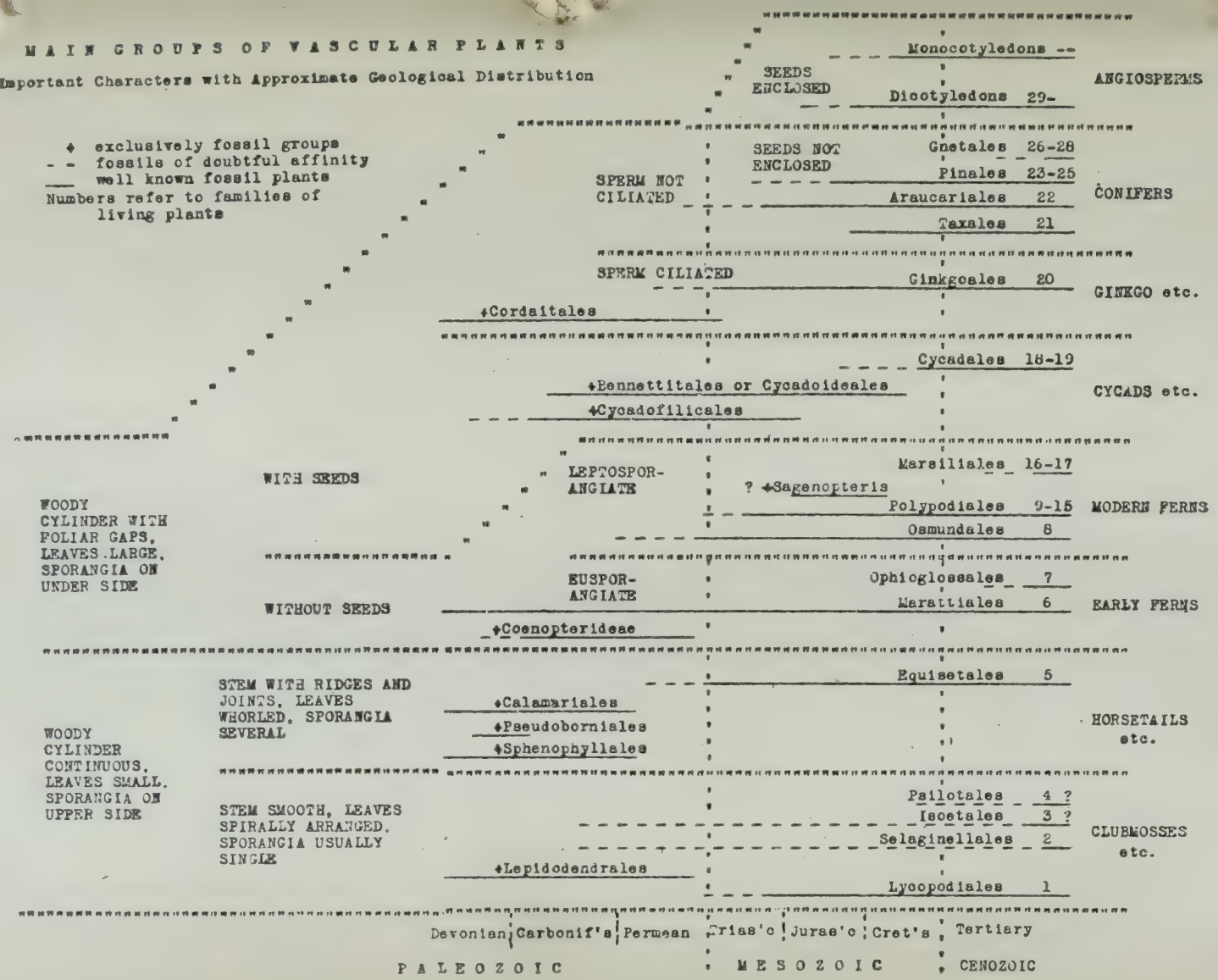
If after a period of years, preferably longer than ten, a different set of numbers should be adopted, this would only very slightly interfere with their benefits. Possibly alternate lists might make needed changes by inserted letters a, b, c as has been done by Engler. In any case hardly more than a pamphlet would be required to refer from the ten or twelve thousand genera of vascular plants as ordinarily used directly to family numbers, accompanied by abbreviated family names. The inclusion of genera in an index would not need to imply any recognition of the names. However, at some future time uniform families might naturally lead to an extension of the principle of *genera conservanda*.

An Inventory of Families.

If the desirability of uniform families should be approved by a number of botanists, or if possible by botanical institutions and societies in different countries, something like an inventory of facts and of conflicting opinions which appear to have a bearing on family sequence might be practicable. Such an undertaking would probably clarify many points, whether or not it should result in any world agreement. This would by no means require a re-writing of the *Pflanzenfamilien*. Details of genera and species, except in the cases where these affect the position of a family, would only confuse the issue. Evolutionary sequence is associated with more or less uncertain interpretation of characters; these characters are in nearly all cases very different from those by which plants are identified. Thus limited a survey might be completed within reasonable time. A single volume with a preliminary sequence, indicating the various possible arrangements, might contain more information than great works which include miscellaneous subjects.

The sequence adopted for the diagram on the opposite page is intended to call attention to some of the specific questions involved. The geologic distribution must be considered as only approximate. There are four main changes from the *Pflanzenfamilien* 1° *Lycopodiaceæ* etc. are not interposed between the ferns and seed plants; 2° ferns begin with eusporangiate forms as shown by Bower; 3° the ancient and diversified group of gymnosperms requires a greater number of families, as used by many authors; 4° angiosperms begin with dicotyledons. The families might then begin somewhat as follows:

Lycopodiaceæ	Lycop	1	*Sagenopteris*		
Lepidodendrales			Marsiliaceæ	Mars	16
Selaginellaceæ	Selag	2	Salviniaceæ	Salv	17
Isoetaceæ	Isoet	3			
Psilotaceæ	Psil	4?	*Pteridospermæ*		
			Cycadaceæ	Cycad	18
Sphenophyllales			Zamiaceæ	Zami	19
Pseudoborniales			*Bennettitales*		
Calamariales					
Equisetaceæ	Equis		*Cordaitales*		
			Ginkgoaceæ	Ginkg	20
Coenopterideæ					
Psaronieæ.			Taxaceæ	Taxac	21


MAIN GROUPS OF VASCULAR PLANTS
Important Characters with Approximate Geological Distribution
♦ exclusively fossil groups
- - fossils of doubtful affinity
___ well known fossil plants
Numbers refer to families of living plants
WOODY CYLINDER WITH FOLIAR GAPS, LEAVES LARGE, SPORANGIA ON UNDER SIDE
WITH SEEDS
WITHOUT SEEDS
SEEDS ENCLOSED
SEEDS NOT ENCLOSED
SPERM NOT CILIATED
SPERM CILIATED
LEPTOSPORANGIATE
EUSPORANGIATE
Monocotyledons --
Dicotyledons 29-
Gnetales 26-28
Pinales 23-25
Araucariales 22
Taxales 21
Ginkgoales 20
♦Cordaitales
Cycadales 18-19
♦Bennettitales or Cycadoideales
♦Cycadofilicales
Marsiliales 16-17
? ♦Sagenopteris
Polypodiales 9-15
Osmundales 8
Ophioglossales 7
Marattiales 6
♦Coenopterideae
ANGIOSPERMS
CONIFERS
GINKGO etc.
CYCADS etc.
MODERN FERNS
EARLY FERNS
WOODY CYLINDER CONTINUOUS, LEAVES SMALL, SPORANGIA ON UPPER SIDE
STEM WITH RIDGES AND JOINTS, LEAVES WHORLED, SPORANGIA SEVERAL
STEM SMOOTH, LEAVES SPIRALLY ARRANGED, SPORANGIA USUALLY SINGLE
Equisetales 5
♦Calamariales
♦Pseudoborniales
♦Sphenophyllales
Psilotales 4 ?
Isoetales 3 ?
Selaginellales 2
♦Lepidodendrales
Lycopodiales 1
HORSETAILS etc.
CLUBMOSSES etc.
Devonian
Carbonif's
Permean
Trias'c
Juras'c
Cret's
Tertiary
PALEOZOIC
MESOZOIC
CENOZOIC

Marattiaceæ	Marat 9	Araucariaceæ	Arauc 22
Ophioglossaceæ	Ophio 7	Pinaceæ	Pinac 23
		Taxodiaceæ.	Taxod 24?
Osmundaceæ	Osmun 8	Cupressaceæ	Cnpr 25
Gleicheniaceæ	Gieich 9	Ephedraceæ	Ephed 26
Matoniaceæ	Maton 10	Welwitschiaceæ	Welw 27
Hymenophyllaceæ	Hymen 11	Gnetaceæ	Gnet 28
Schizæaceæ	Schiz 12		
Ceratopteridaceæ	Cerat 29	DICOTYLEDONS 29—	
Cyatheaceæ	Cyath 14		
Polypodiaceæ		MONOCOTYLEDONS.	

Seeking a maximum of stability it is not desirable to assign numbers to exclusively fossil groups. For the same reason groups such as ferns or monocotyledons are not numbered separately; the position or delimitation of such groups may be different in the future. But with a single series as of vascular plants, possibly later extended to all plants, the numbers would be essentially *symbols*; periodic changes due to improved classifications would require practically no new names, only a reassignment of numbers. In the case of a few very large families, such as the Compositæ, it might be preferable that the numbers should refer to tribes. The thought is here of the co-ordination of information rather than of the arrangement of collections.

The angiosperms in the *Pflanzenfamilien* are arranged according to a rigid system of floral morphology. Among questions which would need to be considered in a possible rearrangement are:

(*a*). Whether woody plants should generally precede herbaceous ones within a given relationship;

(*b*). Whether at least apetalous herbaceous plants should follow related polypetalous ones;

(*c*). Whether *Piperales* should be removed from its position between *Casuarinaceæ* and *Salicaceæ* to a later position perhaps near *Polygonaceæ*;

(*d*). Whether *Proteaceæ* should be nearer the earliest angiosperms;

(*e*). Whether *Aizoaceæ* and *Cactaceæ* are related;

(*f*). Whether *Caryophyllaceæ*, *Linaceæ* and *Gentianaceæ* are related;

(*g*). Whether *Cornaceæ* should be near *Caprifoliaceæ*;

(*h*). Whether *Cucurbitaceæ* should be near *Passifloraceæ*;

(*i*). Whether groups such as *Mimoseæ*, *Clusieæ*, *Cichorieæ* etc. should be considered as families;

(*j*). Whether *Alismaceæ* are the primitive monocotyledons;

(*k*). What are the relationships of the *Palmæ*;

(*l*). Whether *Araceæ* are related to *Piperaceæ*.

SUMMARY.

The present article may be briefly summarized:

1. A periodic inventory of facts and opinions which appear to have a bearing on the sequence of families, especially of living vascular plants, is greatly to be desired.

2. Where facts are not conclusive the definite goal of a truly international sequence should be sought through agreement.

3. Standard numbers as part of symbols for plant families, revised at suitable intervals, would serve important practical purposes, especially in the co-ordination of information.

In conclusion it may be said that if it should be widely agreed that an international family sequence were desirable, ways would doubtless be found to overcome the various difficulties in the way of its establishment. Discussion of the subject by those interested might be a first step.

BROOKLYN BOTANIC GARDEN.

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THE EVOLUTION OF PRIMITIVE PLANTS FROM THE GEOLOGIST'S VIEWPOINT.

By Charles Schuchert.

THE writer has read with a great deal of profit A. H. Church's recent valuable memoir, "Thalassiophyta and the Subaerial Transmigration"[1] and A.G.T.'s clear and searching review of it, "The Evolution of Plants."[2] Church's paper is of great importance not only to all botanists, but to all teachers of Historical Geology as well, and the writer, as a member of the latter group, is thankful to him for having written it. As paleontologists we may accept his conclusions and leave to the botanists the discussion as to the course of evolution the marine algæ took in their ascent to land plants. As a paleontologist and geologist, however, the writer cannot accept some of Church's geologic dicta, and since the editor of the New Phytologist invites criticism, the following questions may be raised.

First, did the earth ever have a universal ocean? Second, has the amount of water in the hydrosphere decreased or increased during the geological ages? Third, was the primal ocean as salty as it is to-day, and what is the source of these salts?

The answers to these questions must be sought in the light of what is going on in the world about us and of what the astronomers, geophysicists, and geologists tell us about the evolution of the galaxy and of the constellation of the sun, and the origin of the earth. The famous Laplacian theory of earth origin, adapted by the elder Dana to the earliest stages of earth evolution, is now badly shattered, and out of it has risen a new one, the Chamberlin-Moulton planetesimal hypothesis. In accordance with this later theory, the earth never was a star that finally became encrusted with a rocky surface, above which floated an atmosphere holding all the water now on the earth's exterior and that which has percolated to the exterior portion of the lithosphere during the geologic ages. The universal ocean of the ancients, fastened upon geology more than a century ago by Werner, was a figment of his imagination. On the contrary, the earth's oldest surface, probably never to be discovered, was composed of far more dry land than water. Ocean basins in the sense of those of to-day may then not have existed. All of the water on the face of the earth has been

[1] *Oxford Botanical Memoirs* **3**, 1919. Oxford Univ. Press. Price 3s. 6d.

[2] New Phyt. **19**, 1920, p. 1.

slowly liberated by the earth itself, as "juvenile water," through its volcanoes and thermal springs. What we see to-day of vadose (=old) waters is the accumulation of more than one thousand million years. Likewise the salts of the seas and oceans have been of slow gathering, for they have been gradually washed out of the land and have accumulated in the oceanic basins during the great length of geologic time. The rivers of to-day are known to be variably saline, and it is their small daily additions to the seas that have gone towards making up the vast amounts of salts contained in the latter, locked up in the rocks as rock-salt, or forming part of the enormous limestone and dolomite beds of the geologic formations. This subject is treated in detail in Chamberlin and Salisbury's "Geology" or in shorter and more popular form in "The Evolution of the Earth and its Inhabitants," a series of papers by Yale instructors.

We now know that the oceans did not always remain within their confines as at present delimited, for the many well known fossiliferous deposits on the continents attest that the marine waters have been over the latter. Since the beginning of the Paleozoic, the oceans have repeatedly flooded the lands more or less widely, but never have all the lands of any one time been beneath the seas. What has been true since the Cambrian was probably equally so for Archeozoic and Proterozoic times; but with this difference, that the water basins and the continental protuberances in the Archeozoic were probably smaller and by far greater in number than they are to-day.

What is the bearing of these statements on Church's theory? Certainly they do not disprove his conclusions, rather do they appear to make all the more easy the solutions along his lines of thinking. We may therefore agree with him that nearly all life in the earliest Archeozoic consisted of oceanic micro-plankton, but that the oceans did not then have their present depth and that there were lands with shores and shallow-to-littoral seas, with sunlit bottoms, just as there are to-day. Accordingly some of the plankton, after it had evolved into nucleated cells living in colonial form, might easily have found a bottom where assimilation could have been continued, though probably more slowly than in the surface waters. With the finding of this favorable bottom for the continuance of life, a new factor in organic environment was introduced, and out of the struggle for adaptation to it there arose the plant benthos.

We know that a far greater variety of life is found in the salty waters of the seas and oceans than is the case in the fresh waters of the present and the past. The many kinds of salts in the oceans appear to be a stimulus toward individual and specific differentiation. To-day the marine waters have about 3·5 per cent of salts and three quarters of these are sodium chloride. This present quantity, however, is, as has been said, the accumulation of the geologic ages, and from this conclusion it follows that the Archeozoic oceans had far less salts and probably a different salt combination. It is likely that at all times the oceans were salty, but in late Archeozoic time the amount may not have risen to one half what it is now. The lime and magnesium salts in solution may have been at first far greater in quantity than at present, but as soon as denitrifying bacteria came into existence, the warm water oceans were probably freed of their lime sulphates as quickly and as thoroughly as they are at present. It would also appear that the oceans originally received far less nitrogen from the lands than they do now, since the continents of Archeozoic time had no land plants to assist in taking this element out of the atmosphere and in turn furnishing it to the rivers to transport to the seas.

Church is very positive that the primitive lands could have had no soils and that everywhere there was a hard rock surface until they were clad with verdure. But an earth with an atmosphere holding water vapor was bound at once to break down the rocks and so to form soils. The sediments of the Archeozoic formations were derived from crystalline rocks, the original source of all sedimentary strata. Their nature is like that of the Proterozoic sediments, and since these latter are far less metamorphosed, it can be definitely stated that a study of them leads to the conclusion that the lands must have had, ever since there was an atmosphere and rain, arkoses (broken up crystalline rocks without chemical alteration) and soils, for if not, whence came the marine sediments? Of course these primitive soils had no humus in them, for there was no land life from which this could be made, but we can depend upon it that along the seashore and in the marine swamps the detritus of the land was most comminuted and also more or less changed chemically. Here the waves would wash out, and the wind distribute, some of the moribund life of oceans, and therefore land humus had its origin at the sea margin. With the adaptation of the hardier marine seaweeds to these marginal strips of shore, the *transmigration* of the plants of the oceans over the lands was begun.

A far more favourable condition for this transmigration is to be sought in the variable nature of the sea-level, due to crustal movement. We know that during the Paleozoic the oceans invaded North America at different times to the extent of millions of square miles. These overfloodings were shallow seas—epeiric seas—with an average depth of probably less than 500 feet. Now think of these seas withdrawing very slowly from the land, and see what a favorable ground for humus must have been left in their wake, where the seaweeds might become adapted to the new environment that was thus forced upon them. Just as the fishes had to develop legs and lungs if they were to become the land-living amphibia of the Silurian or Devonian, so the Thalassiophyta, probably as early as the Archeozoic, were forced to become Xerophyta.

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PRELIMINARY NOTE ON A HYDRION DIFFERENTIATION THEORY OF HELIOTROPISM.

BY JAMES SMALL, D.Sc.

FURTHER work, which is now proceeding on the influence of carbon dioxide on geotropism and heliotropism, having indicated that the carbon dioxide balance is, indeed, of the fundamental importance previously suggested (1, p. 51 and 2, p. 208), a hydrion differentiation theory of heliotropism has been developed As it will be some time before the experimental work now in progress can be completed, the theory has been considered of sufficient interest in itself to warrant a brief description.

It has been suggested, and there is more experimental evidence accumulating in support, that the direction of geotropic curvatures is governed by the hydrion concentration of the continuous phase of the plasma membranes of the perceptive cells. The present theory is that the same is true for heliotropic curvatures.

Briefly, it is suggested that light, either by increasing photosynthesis and the amount of respirable material or more probably

in some other way, increases the rate of respiration in the perceptive cells. This increase in respiration involves an increase in the carbon dioxide within the cells affected. Such an increase in carbon dioxide involves in "root" structures an increased hydrion concentration of the already relatively acid continuous phase of the plasma membranes, giving increased relative acidity with consequent increase in polarisation and in turgidity. Root structures, therefore become more turgid on the side which is more illuminated, and show negative heliotropism.

The increase in carbon dioxide within the perceptive cells in "stem" structures involves an increased hydrion concentration of the already relatively alkaline continuous phase of the plasma membranes, giving decreased relative alkalinity with consequent decrease in polarisation and in turgidity. Stem structures, therefore, become less turgid on the side which is more illuminated, and show positive heliotropism.

Since this explanation of heliotropism holds for non-chlorophyllous roots, fungi, sporogonium stalks (e.g., *Pellia*), etc., as well as for chlorophyllous structures, it is more probable that light reacts directly on the amount of respiratory carbon dioxide, rather than indirectly by increasing the amount of respirable material. This aspect, as well as others, is now receiving attention, and reversed curvatures both geotropic and heliotropic have been obtained in atmospheres containing a large percentage of carbon dioxide.

Botanical Department,

October 28th, 1920. The Queen's University of Belfast.

1. Small, J. A Theory of Geotropism, New Phytologist, Vol. XIX., p. 49.
2. Small, J. and Rea, M. W. Preliminary Notes I. On the Reversal of Geotropic Curvature of the Stem. Ibid. Vol. XIX., p. 208.

REVIEW

"Fossil Plants. A Text Book for Students of Botany and Geology." By A. C. Seward. Vol. IV, Cambridge, 1919, pp. XVI and 543, Figs. 630—818.

THE fourth and last volume of Professor Seward's text book of palæobotany completes the account of the fossil Gymnosperms, including the Ginkgoales, Coniferales and Gnetales. The Ginkgoales, which formed a considerable element of many past floras, are fully treated, but they are known mainly by leaf impressions, the abundance of which makes it surprising that so little is known of other parts of the plant. There are scarcely even any reliable records of fossil Ginkgoalian wood. A short chapter at the end of the book is sufficient for supposed fossil examples of the Gnetales, none being of any great botanical importance, and the main part of the book is devoted to the Coniferales, introduced by a very valuable and well-illustrated chapter on recent conifers.

In dealing with fossil forms, the foliage shoots and reproductive organs, though often difficult to correlate, are described together by Professor Seward as far as possible under each family, with an additional chapter for wholly doubtful genera, while the wood is given separate treatment. This arrangement is undoubtedly the best in the present state of palæobotanical knowledge, which makes it very difficult to get a connected idea of the plant as a whole, a difficulty which is reflected in the nomenclature used by palæobotanists, necessitating the use of provisional "generic rubbish-heaps" such as *Brachyphyllum* and *Pagiophyllum*, and the multiplication of "genera" for different organs of what may be the same plant. The use of the same name for sterile branches and for unconnected cones has in the past added considerably to the confusion, and the present exhaustive work has reduced to something like order the terminological chaos which enveloped the numerous fossil impressions of twigs, leaves and cones, and will considerably lighten the task of all future workers.

The classification of fossil coniferous woods as revised by Gothan is accepted with some modifications by Professor Seward, who thinks that Gothan has carried generic subdivision too far. For example, he substitutes a new name, *Mesembrioxylon*, for the two genera *Podocarpoxylon* and *Phyllocladoxylon*. These two groups are certainly very difficult to distinguish, even when the preservation is perfect, and it is perhaps best for the present not to attempt to separate them, but Professor Seward's view of the implications of the names would probably not be admitted by Dr. Gothan. Speaking of *Podocarpoxylon* and *Phyllocladoxylon* (p. 203) he says "the use of Gothan's names implies affinities to recent genera which there are no adequate reasons for assuming," yet on another occasion he himself states that "the fossil wood described under *Cedroxylon* does not denote that the parent plants were more closely allied to *Cedrus* than to some other genera of the same family" (p. 369), which seems to be the most satisfactory view to take of all such names. And if fossil woods have been too

minutely subdivided, there seems no very strong reason for retaining such a genus as *Planoxylon*, which has no characters by which it may be distinguished from *Protocedroxylon*, a name accepted by Professor Seward without comment, though Dr. Stopes considers that it is objectionable on the ground of unfounded implications of affinity.

A consideration of the evidence so carefully brought together and arranged by Professor Seward shows that we are not yet in a position to give conclusive answers to the many interesting problems connected with the phylogeny of the Coniferales. While stating that the group is probably monophyletic, Professor Seward refrains from giving any decisive opinion as to the stock from which it sprang. He thinks that the weight of evidence is in favour of the Araucarineæ being older than the Abietineæ, but that at present we can say little more definite than that the latter had a later maximum development than the former. The evidence from foliage shoots and cones is somewhat uncertain, but the fossil wood points to the Araucarineæ as being older, though Cordaitean and Arancarian woods have not yet been satisfactorily separated. Professor Seward is very cautious about most supposed pre-Jurassic Araucarians, though he thinks that many forms (*e.g.* of *Walchia*. *Voltzia* and *Ullmannia*) show undoubted Araucarian affinities. He concludes that the *Araucaria* type is older than that of *Agathis* (*Araucarites Delafondi* from the Permian is one of the earliest definite examples of an araucarian cone-scale), and points out that this once cosmopolitan family continued to flourish in the northern hemisphere till well into the Tertiary period.

It is unfortunate that the Podocarpineæ, which may be allied to the Araucarians, are very unsatisfactorily represented in the geological sequence, and records of undoubted Taxineæ are also very rare. The Cupressineæ and Abietineæ were abundant in later Mesozoic times, though correlation with living genera is difficult, and there are many fossil forms which cannot even be placed with certainty in any particular family. It is to be hoped, as Professor Seward suggests, that the cuticular study of these impressions will be of some help in classification, for little has been done in this direction so far.

In conclusion, one may say that this volume marks a definite stage in our knowledge of the past history of the conifers, and it indicates clearly the gaps which must be filled in by future investigation. It is a matter for regret that the fossil Angiosperms are not yet ripe for similar treatment, and that this important work is now concluded, but all botanists will look forward eagerly to Professor Seward's promised general survey of past floras, which could not be included in a descriptive text book.

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